Variabilidad funcional de *Prosopis pallida* frente a factores climáticos y edáficos en un gradiente ambiental en la costa norte de Perú

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TITULO: *VARIABILIDAD FUNCIONAL DE PROSOPIS PALLIDA FRENTE A FACTORES CLIMÁTICOS Y EDÁFICOS EN UN GRADIENTE AMBIENTAL EN LA COSTA NORTE DE PERÚ*

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TESIS DOCTORAL

Variabilidad funcional de *Prosopis pallida* frente a factores climáticos y edáficos en un gradiente ambiental en la costa norte de Perú

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Directores: Rafael Villar Montero y Rafael Navarro Cerrillo

Córdoba, 18 de Enero de 2018

Programa de Doctorado Recursos Naturales y Sostenibilidad

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TÍTULO DE LA TESIS:

Variabilidad funcional de *Prosopis pallida* frente a factores climáticos y edáficos en un gradiente ambiental en la costa norte de Perú

DOCTORANDO: Pablo César Salazar Zarzosa

INFORME RAZONADO DEL/DE LOS DIRECTOR/ES DE LA TESIS

El tema principal de esta tesis se centra en el estudio de la variabilidad intraespecífica de *Prosopis pallida* (algarrobo) y su respuesta a los factores climáticos y edáficos en Perú. La tesis consta de 7 capítulos: una introducción general, 5 capítulos experimentales y una discusión general.

El trabajo engloba muchos aspectos importantes para entender el funcionamiento de distintas poblaciones de *Prosopis pallida* a lo largo de un gradiente climático. Entre estos aspectos están: a) la respuesta del crecimiento de los anillos al fenómeno del Niño; b) la respuesta de plántulas (crecimiento, distribución de biomasa, estructura de la hoja e intercambio gaseoso) a la distinta disponibilidad de agua, c) la variación intraespecífica en los rasgos funcionales de la hoja, d) la variación en la concentración de nutrientes del suelo y su repercusión en la concentración de nutrientes de la planta y e) el efecto de isla de fertilidad del algarrobo. Esto da idea de las distintas temáticas teóricas y metodológicas que Pablo C. Salazar ha tenido que desarrollar y llegar a dominar. Además, Pablo C. Salazar ha aprendido numerosos test estadísticos, llegando a dominar el entorno R.

Un capítulo está publicado en la revista *Journal of Arid Environments*, revista internacional dentro de la categoría de *Ecology/ Environment* y que es la revista de referencia de los ecosistemas áridos. Otros dos capítulos están actualmente en revisión en dos revistas internacionales (*Forestry* y *Catena*) de las categorías de *Forestry* y *Soil Sciences*. Además, gran parte de estos resultados se han divulgado en varios congresos nacionales e internacionales, como el XIII Congreso de ecología de la Asociación española de Ecología terrestre en Portugal, 4º congreso ibérico de ecología en España, y el Congreso Internacional del Cambio Climático y sus Impactos en Perú.

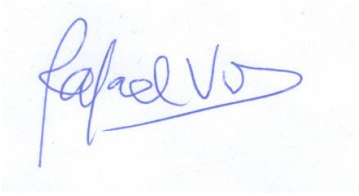
Los resultados de la tesis son muy interesantes y novedosos, ya que permiten conocer aspectos básicos del funcionamiento del algarrobo, que pueden ser importantes para su conservación y gestión.

Otro mérito adicional es que la tesis es el producto del proyecto de investigación del cual Pablo C. Salazar fue uno de los redactores. La tesis ha conllevado un enorme esfuerzo de muestreo y análisis, ya que se ha realizado en un área amplia cubriendo 8500 km^2, con parcelas distantes y conectadas por carreteras secundarias y caminos forestales y con un clima cálido y seco que ha conllevado un esfuerzo adicional. Todo esto ha sido posible gracias a que Pablo C. Salazar tiene una capacidad de trabajo impresionante y ha sido capaz de llevar adelante todo el trabajo de su Tesis con entusiasmo y alegría. A todo esto se añade la distancia física entre el doctorando y sus directores (más de 9000 km), una dificultad añadida que ha superado con creces.

Por todo ello, se autoriza la presentación de la tesis doctoral.

Córdoba, 18 de enero de 2018

Firma de los directores



Fdo.: Rafael Villar Montero

Fdo.: Rafael M. Navarro-Cerrillo

INFORME SOBRE APORTACIONES DERIVADAS DE LA TESIS DOCTORAL Y FACTOR DE IMPACTO DE LAS REVISTAS CIENTÍFICAS (JOURNAL CITATION REPORTS)

Publicaciones en revistas científicas (Capítulo de la tesis doctoral)

Salazar Zarzosa, P., Navarro-Cerrillo, R., Cruz, G., Villar, R. (2018). Intraspecific leaf functional trait variability of eight *Prosopis pallida* tree populations along a climatic gradient of the dry forests of northern Peru. Journal of Arid Environment aceptado. (**Capítulo 4**).

Factor de impacto: 1.8, Posición de la revista en relación a su categoría específica (Environment/Ecology) 65/341; Primer cuartil (Q1)

Manuscritos enviados a revistas científicas (Capítulo de la tesis doctoral)

Salazar Zarzosa, P., Navarro-Cerrillo, R., Ancajima, E., Duque Lazo, J., Rodríguez, R., Ghezzi, I. and Mabres, A. (2018) Variation of the ENSO effects on Prosopis pallida forests along a climatic gradient. Manuscrito enviado a la revista "Forestry: An International Journal of Forest Research." (**Capítulo 2**)

Factor de impacto: 2.2, Posición de la revista en relación a su categoría específica (Plant and Animal Science) 252/773; segundo cuartil (Q2)

Salazar Zarzosa, P., Navarro-Cerrillo, R., Grados, N., Cruz, G., Villar, R. (2018) Can the "fertility island" effect be restricted in *Prosopis pallida* populations? Manuscrito enviado a la revista "Catena" (**Capítulo 6**)

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Olmo M, Villar R, **Salazar P**, Alburquerque JA (2015) Changes in soil nutrient availability explain biochar's impact on wheat root development. Plant and Soil. DOI 10.1007/s11104-015-2700-5.

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Proyectos de investigación formulados y financiados

146-Fincyt-IB-2013. Rasgos funcionales de las poblaciones locales de algarrobo (*Prosopis pallida*) y su influencia sobre los servicios ecosistémicos en las principales comunidades rurales del norte de Perú. Financiado por Innovate Perú. Presupuesto concedido: 102289 euros. Duración 3 años: 2013-2016.

404-PNICP-PIBA-2014. Estudio de parámetros biológicos en *Prosopis* sp. como un registro paleoclimático: Fundamentos y uso de nuevos métodos de medición dendrocronológica. Financiado por Innovate Perú. Presupuesto concedido: 102264 euros. Duración 3 años: 2014-2017.

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El presente trabajo se ha realizado en el marco del Proyecto de Investigación 146-Fincyt-IB-2013. Rasgos funcionales de las poblaciones locales de algarrobo (*Prosopis pallida*) y su influencia sobre los servicios ecosistémicos en las principales comunidades rurales del norte de Perú financiado por Innovate Perú.

Así mismo, los proyectos españoles del Ministerio de Economía y Competitividad (MEC) DIVERBOS (CGL2011-30285-C02-02); ECO-MEDIT (CGL2014-53236-R) y QUERCUSAT (CGL2013-40790-R); y los fondos europeos FEDER han participado en la financiación de esta tesis doctoral.

Gracias por estar a mi lado a pesar de la adversidad.

A mi esposa

“No hemos venido a este mundo a divertirnos.

Estamos aquí para aprender” – Mi Mamá

Resumen

Las zonas áridas del mundo representan el 36-40% de la superficie continental del planeta, contienen el 10% del stock de carbono del planeta, y son el hogar de más de 2000 millones de personas. El algarrobo (*Prosopis pallida*) es una especie nativa de las zonas áridas de la costa oeste de América, y en Perú representa la principal especie arbórea de los bosques secos. La costa norte del Perú es su principal zona de distribución, donde alcanza más del 60% de la cubierta forestal de la región.

Esta zona es, además, uno de los puntos de mayor impacto del fenómeno El Niño (ENSO – del inglés *El Niño Southern Oscillation*), el cual genera una "fase seca" con largos periodos de sequía (con menos de 300 mm de precipitación anual) y una "fase húmeda" con cortos periodos húmedos (con más de 1000 mm anuales). La complejidad climática, junto con el pH alcalino y la textura arenosa del suelo, hacen de este territorio un lugar hostil para la vegetación, que requiere tanto de adaptaciones a condiciones pobres en nutrientes como de una respuesta plástica a la falta y exceso de agua.

El objetivo de esta tesis es conocer la variabilidad intraespecífica de las principales poblaciones de algarrobo presentes en la región norte de Perú en respuesta a la variabilidad espacio-temporal del clima y a las características edáficas. Para ello, se seleccionaron 8 poblaciones de algarrobo a lo largo de un gradiente climático en la costa norte de Perú (región de Piura), y se realizaron experimentos de campo e invernadero donde se midieron características morfológicas y fisiológicas del algarrobo en respuesta a la variabilidad climática natural y también en condiciones controladas. Además, analizamos la variabilidad en las características físicas del suelo y la concentración de nutrientes en suelo y hoja, así como el efecto de la proximidad al árbol sobre la concentración de nutrientes en el suelo (efecto isla de fertilidad).

En el **capítulo 2** exploramos la variabilidad temporal del crecimiento mediante análisis dendrocronológicos en 3 de las poblaciones seleccionadas a lo largo del gradiente climático. Las series de crecimiento de los anillos demostraron que el algarrobo es una especie plástica, cuyo crecimiento puede aumentar hasta 4 veces más durante el ENSO en comparación a años normales. El crecimiento radial se correlacionó positivamente con la precipitación y la temperatura de verano, así como con la temperatura del mar, la cual controla la climatología de la región a través de la corriente de Humboldt. El crecimiento, y su relación con el clima, fueron

significativamente diferentes entre las poblaciones. Los bosques costeros registraron una menor variabilidad en el tamaño de los anillos y una menor correlación con la temperatura y la precipitación, mientras que el crecimiento de las poblaciones localizadas más al interior se correlacionó significativamente con la temperatura y la precipitación, y presentaron anillos de mayor tamaño en años de ENSO. Esto demuestra que el algarrobo es una especie muy plástica que responde a la variabilidad espacio-temporal del clima.

En el **capítulo 3** analizamos la plasticidad fenotípica del algarrobo frente a la disponibilidad hídrica en condiciones de invernadero en 7 poblaciones. Los resultados indican que la respuesta a la disponibilidad hídrica es compleja con una modificación estructural de la hoja y de la proporción de raíz que se relaciona con un aumento de la evapotranspiración y la biomasa total. En general, la plasticidad fenotípica fue diferente entre poblaciones y no se correlacionó con el gradiente de climático. Sin embargo, la plasticidad en la eficiencia instantánea del uso del agua presentó una correlación negativa con la precipitación y positiva con el índice de sequía SPEI (standardized precipitation-evapotranspiration index) del lugar de origen.

En el **capítulo 4** se estudió la variabilidad intraespecífica de los rasgos funcionales en hojas del algarrobo durante la fase seca en las 8 poblaciones. Los resultados obtenidos indican que el algarrobo presenta una alta variabilidad intraespecífica y sigue la tendencia del espectro económico global de la hoja. La descomposición de la varianza indicó que las variables estructurales, como el peso específico foliar y el contenido en materia seca de la hoja, presentaron su mayor variabilidad a nivel de población, mientras que las variables de intercambio gaseoso y la composición química de la hoja presentaron mayor variabilidad a nivel de parcela y árbol. La temperatura fue la principal variable correlacionada con las variables relacionadas con la regulación hídrica de la hoja. Así, la temperatura media anual se correlacionó negativamente con el contenido relativo de agua en hoja y el tamaño del estoma, y positivamente con la eficiencia instantánea en el uso del agua.

En el **capítulo 5** se estudió la variabilidad en las características y concentración de nutrientes en el suelo, así como su relación con la estequiometría de nutrientes en hoja en 8 poblaciones. Los resultados indican que los nutrientes en el suelo mantienen una relación común, generando un gradiente de fertilidad que no se relaciona con la variabilidad climática. Las

características del suelo, como el pH y la conductividad eléctrica estaban relacionadas con la concentración de nutrientes de la hoja. Así, el pH del suelo se correlacionó positivamente con la relación Ca/C y Cu/C foliar, y negativamente con la relación N/C y el P/C de la hoja. Por otro lado, la conductividad eléctrica se correlacionó positivamente con la relación K/C y Cu/C foliar, y negativamente con la relación Fe/C y Mn/C de la hoja. Esto indica que las características del suelo regulan la nutrición vegetal, especialmente el fósforo, el cual también se correlacionó positivamente con la fertilidad del suelo. Además, encontramos una correlación negativa entre la concentración de manganeso foliar y la concentración de nutrientes del suelo en 7 de los 10 elementos estudiados, sugiriendo que el Mn en la hoja puede usarse como indicador de la fertilidad del suelo en el bosque seco.

En el **capítulo 6** analizamos el efecto de la isla de fertilidad del algarrobo mediante el análisis de la concentración de nutrientes del suelo fuera y dentro de la copa del árbol en 5 poblaciones a lo largo del gradiente climático. Aunque encontramos un efecto positivo de la isla de fertilidad, el incremento de nutrientes en el suelo, basado en la cercanía del árbol, fue pequeño. En cambio, el tamaño del árbol (altura, área de copa), la estructura y la composición química de la hoja presentaron una correlación positiva con la concentración de nutrientes en suelo y son, por tanto, factores determinantes en el efecto de la isla de fertilidad. Al igual que en capítulos previos encontramos diferencias en el efecto de la isla de fertilidad entre las poblaciones, de modo que poblaciones con menor temperatura y mayor precipitación, tendrán una mayor concentración de nutrientes en el suelo.

En resumen, esta tesis demuestra que el algarrobo es una especie muy plástica, capaz de modificar su crecimiento y su fisiología de acuerdo a la variabilidad espacio-temporal del clima durante la fase seca y húmeda generada por el ENSO, así como también con la variabilidad espacial de las características y fertilidad del suelo. Finalmente, estas diferencias alteran el efecto de la isla de fertilidad del algarrobo y su impacto sobre los nutrientes en el suelo. Por tanto, los resultados de esta tesis demuestran que el algarrobo es una especie importante para los programas de conservación en zonas áridas del norte de Perú, cuya variabilidad puede ser clave en la recuperación de zonas degradas y en el estudio del cambio climático.

Abstract

Dryland ecosystems represent 36-40 % of the planet land cover, it holds 10% of the planet carbon stock, and it is the home of 2000 million people. The algarrobo (*Prosopis pallida*) is a native species of the American coast, and in Peru, it is the main tree species in the dryland forest. It is mainly located in the North Peruvian dryland forest, where it can reach 60% of the region vegetation cover.

This location is also a hotspot for the monitoring of El Niño-Southern Oscillation (ENSO), which generates a "dry phase" with long drought season (less than 300 mm annual rainfall) and a "wet phase" with a short rainy season (more than 1000 mm annual rainfall). This complex climatic scenario, alongside the high pH and the sandy texture of the soil, makes this location a hostile territory for plant life, which requires adaptations to poor nutrient soil as well as a plastic response to the water availability.

The main objective of this thesis is to know the intraspecific variability of the main algarrobo populations in the Northern Peruvian dryland forest and its relationship with the spatial-temporal climatic and edaphic variability. For that, we selected 8 algarrobo populations along a climatic gradient in the North Peruvian coast (Piura region), and we conducted field and greenhouse experiments to measure morphological and physiological characteristics of algarrobo and its response to the climatic variability and water availability under controlled conditions. Moreover, we analysed the variability of soil characteristics and soil and leaf nutrient concentration, together with the effect of the proximity of the tree on the soil nutrient concentration (fertility island effect).

In **chapter 2**, we explore the temporal variability of plant growth through dendrocronological analyses in three populations of algarrobo. The tree ring width series showed that algarrobo is a plastic species able to grow 4 times higher during ENSO events than in average years. Radial growth was correlated positively to summer rainfall and precipitation, as well as sea surface temperature, which control the regional climate through the Humboldt Current. Plant growth and their relationships with the climatic variables were different between populations. Coastal populations showed lower variability of tree ring width and they were less sensitive to climatic variations than inland populations. This demonstrates that algarrobo is a

plastic specie able to respond to the spatial and temporal variations related to ENSO conditions.

In **chapter 3**, we analysed the phenotypic plasticity to water availability through a greenhouse experiment using 7 populations of algarrobo. The results showed that the plastic response to water availability is complex with changes in the leaf structure and root biomass allocation, which are related to an increase in evapotranspiration and plant biomass. In general, phenotypic plasticity was different among populations, and it was not related with the climatic gradient. Regardless, only phenotypic plasticity of water use efficiency showed a significant negative correlation with precipitation and positive with the drought index SPEI (standardized precipitation-evapotranspiration index) from the place of origin.

In **chapter 4**, we studied the intraspecific variability of the leaf functional traits during the ENSO-dry phase in 8 populations across the climatic gradient. The results indicate that algarrobo has a high spatial intraspecific variability and follows the trend of the leaf economic spectrum. The relative variance decomposition showed that population level was the main source of variation for leaf structure, whereas the plot and tree level were the main source of variation for gas exchange traits and leaf chemical composition, respectively. The temperature was the main environmental factor correlated to water regulation variables in the leaf. Thus, the mean annual temperature was negatively correlated with the relative water content of the leaf and the stomata size, and positively with the instantaneous water efficiency.

In **chapter 5**, we studied the variability of the soil properties and the soil nutrient concentration, as well as its relationship with leaf nutrient concentration in 8 populations. The results showed that soil nutrients are tightly related, thus it creates a fertility gradient that is not related to geographic or climactic factors. Soil characteristics, such as pH and electrical conductivity, were related to the concentration of leaf nutrients. Thus, the pH of the soil was correlated positively with the leaf ratio Ca/C and Cu/C, and negatively with the ratio N/C and the P/C of the leaf. On the other hand, the electrical conductivity was correlated positively with the ratio K/C and Cu/C of the leaf, and negatively with the ratio Fe/C and Mn/C of the leaf. This indicates that soil characteristics regulate plant nutrition, especially phosphorus, which also correlated positively with soil fertility. In addition,

we found a negative correlation between leaf manganese concentration and soil nutrient concentration in 7 of the 10 elements studied, suggesting that the Mn in the leaf can be used as an indicator of soil fertility in the dry forest.

In **chapter 6** we analysed the algarrobo fertility island effect based on the soil nutrient concentration outside and inside the tree canopy cover in 5 populations. Even though algarrobo proximity showed a positive effect on soil nutrient concentration, the increase on soil nutrients was not very high. Instead, the fertility island effect was the mainly affected by plant size (height, tree canopy area), leaf structure and chemical composition, which showed a positive correlation with soil nutrient concentration. Once again, the fertility island effect was different between populations, and showed a higher effect in cooler and moister locations.

In summary, this thesis showed that algarrobo is a plastic species able to change its growth and leaf physiology depending on the spatial and temporal variation of the dry phase and wet phase of the ENSO, as well as on the spatial variability of soil fertility and its properties. Finally, these differences alter the effect of the fertility island of the algarrobo and its impact on the soil nutrients. Therefore, these results showed that algarrobo is an important species for conservation programs in the North Peruvian dryland forest, which variability might be key to recover degraded lands and to study climate change.

"La rebelde arena está sometida y el suelo inhóspito esta colonizado. La lúgubre escena de barrios secos está cambiando a anillos verdes. El desolado paisaje sin árboles esta coloreado con pinceladas de marrón, verde y amarillo. La monotonía es cortada por el viajero, y la oveja y la cabra muerden y mastican felizmente las proteínas de la vaina. Los nativos, cuyas tierras fueron quemadas bajo la arena, están agradecidos con el silvicultor y con Prosopis. Y los pobres que no tenían nada que quemar en sus chimeneas ahora tienen Prosopis. Ellos lo recolectaron en su tiempo libre y lo vendieron en los pueblos por un precio decente."

(Reddy, 1978)

Capítulo 1

Introducción general

Esta tesis aborda la variabilidad funcional intraespecífica del algarrobo (*Prosopis pallida* [Humb. & Bonpl. ex Willd.] Kunth) en el bosque seco del Norte de Perú (Fig. 1) donde las variaciones climáticas juegan un papel importante al ser la zona de mayor impacto del Fenómeno el Niño (ENSO, del inglés *El Niño Southern Oscillation*). En esta introducción general se describe, por un lado, el clima en la zona, enmarcado en las zonas áridas del planeta y se explica la importancia de los bosques de algarrobo, así como la influencia del clima en el crecimiento del algarrobo. Por otro lado, se comenta acerca de la plasticidad fenotípica y la variabilidad intraespecífica del algarrobo. Dada la fuerte variación en las variables climáticas, se espera que presente una alta plasticidad fenotípica y exista una gran variabilidad intraespecífica en esta especie. Los dos apartados siguientes se centran en las características del suelo y su papel sobre la disponibilidad de nutrientes en los bosques de algarrobo, así como el efecto de la presencia de los árboles de algarrobo sobre la concentración de nutrientes en el suelo (efecto isla de fertilidad), como un importante servicio ecosistémico que esta especie realiza. Para finalizar, se presentan los objetivos e hipótesis de esta tesis doctoral, así como aquellos aspectos más novedosos.

Figura 1. Algarrobo (*Prosopis pallida*) en el bosque seco aledaño a la laguna de Ñapique.

Las zonas áridas y los bosques de *Prosopis*

Las zonas áridas se caracterizan por tener una baja precipitación, altas temperaturas y alta radiación solar (Reynolds et al., 2007). Esto eleva significativamente la evapotranspiración y el estrés al que se encuentra sometido la vegetación. A esto se suma la baja fertilidad y la calidad de los suelos de estas zonas, que suelen presentar texturas arenosas y pH alcalinos, lo que disminuye significativamente la disponibilidad de nutrientes en el suelo (Pasiecznik et al., 2001). Por todo ello, el paisaje típico de las zonas áridas está representado por parches de vegetación herbácea y arbustiva compuestos por un número limitado de especies (Fig. 2). Su baja biodiversidad suele estar compensada por una alta diferenciación genética entre poblaciones (Martínez-Palacios et al., 1999), confiriéndole una alta resiliencia a factores ambientales. Estas características han convertido a las zonas áridas en laboratorios de campo para estudios de adaptación y resistencia a condiciones extremas (Maestre et al., 2012).

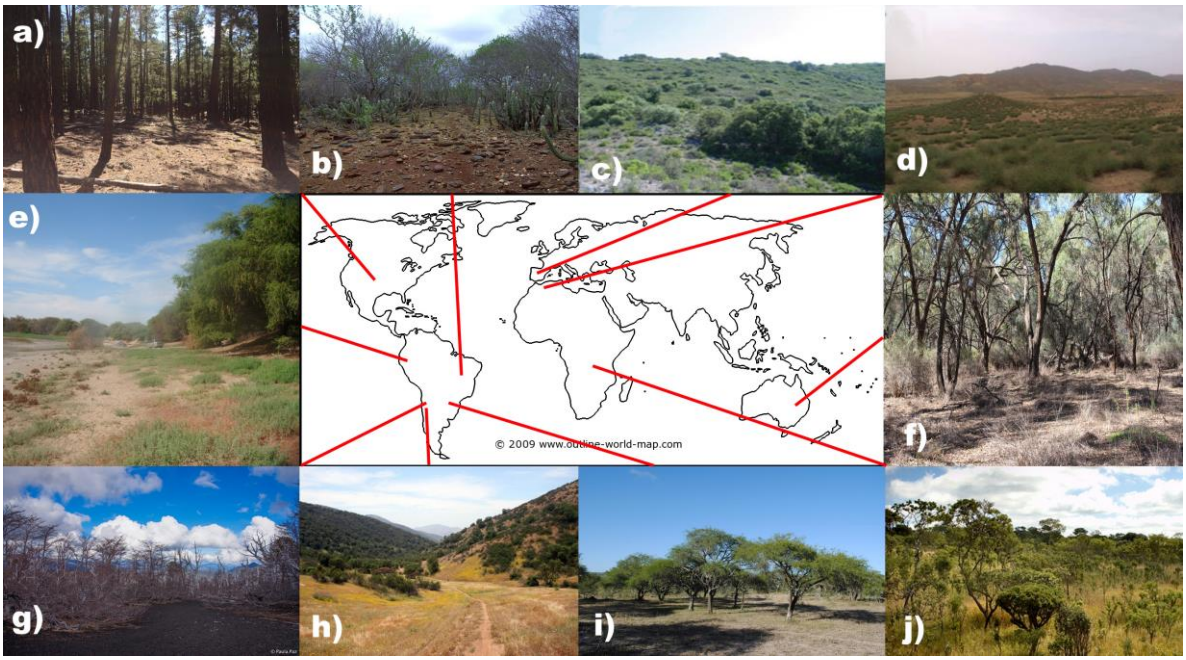

Figura 2. Ejemplos de vegetación en zonas áridas. (a) Bosque denso de pino ponderosa en Arizona, EEUU (b) Bosque seco de Caatinga en Brasil; (c) Matorral dominado por *Quercus coccifera* y *Rosmarinus officinalis* en España; (d) dehesa de *Stipa tenacissima* en Marruecos; (e) Bosque seco de *Prosopis pallida* en Perú; (f) Bosque seco de *Eucalyptus largiflorens* al sur de Australia; (g) Parque Nacional Villarrica en Chile; (h) Matorral espino en Chile; (i) Bosque de *Prosopis nigra* en el chaco seco en Argentina; (j) Bosque seco de Miombo en el norte de Zambia (Adaptado de Maestre et al. 2012).

La importancia de las zonas áridas radica en varios hechos: representan el 36-40% de la superficie continental del planeta, contienen el 10% del stock de carbono mundial, y es el hogar de más de 2000 millones de personas (White et al., 2009). En muchas zonas áridas del mundo se encuentran especies del género *Prosopis*. Originalmente descrito por Linnaeus en 1767, la palabra proviene del griego "pros" que significa "hacia", y "opis", la esposa de Saturno y diosa de la abundancia y la agricultura; y hace referencia a un árbol de gran envergadura y productividad en un ecosistema hostil y desolado. El género está compuesto por 44 especies, de las cuales 40 se encuentran distribuidas en América. La historia taxonómica del género *Prosopis* está llena de definiciones conflictivas y cambios sistemáticos que rara vez llegaron a alterar el esquema taxonómico propuesto por Burkart en 1976 (Pasiecznik et al. 2001). En la actualidad, aún se llevan a cabo estudios genéticos y botánicos para distinguir especies, ecotipos e híbridos (Sherry et al., 2011; Vega y Hernández, 2005); mientras que otros estudios sobre morfología y fisiología buscan determinar las características que confieren a este género su alta resistencia a la sequía (López Lauenstein et al., 2012), la salinidad (Armas et al., 2010), el pH (Goel y Behl, 1995), y a metales pesados (Buendía-González et al., 2010).

De las 44 especies del género *Prosopis*, *P. pallida* (Humb. & Bonpl. ex Willd.) Kunth y *P. juliflora* (Sw.) DC. destacan por su rápido crecimiento, alta productividad y resistencia a la sequía. La distribución natural de estas dos especies se encuentra en la costa oeste de México, Ecuador y Perú (Fig. 3). En Perú, el algarrobo es la especie dominante de las zonas áridas de la costa norte, y es el componente principal de los bosques secos de la región (Burghardt et al., 2010). El algarrobo representa más del 60% de la cubierta forestal en la región de Piura (norte de Perú), y es el sustento de más de 40 mil familias rurales. Su alta resistencia a la salinidad y la sequía hace de él un candidato perfecto para los planes de reforestación en zonas áridas (Deans et al., 2003; Vilela et al., 2003), incluso bajo riego salino (Tomar et al., 2003; Velarde et al., 2003).

Figura 3. Distribución natural del (resaltado en negro) del complejo *Prosopis juliflora-pallida* (modificado de Pasiecznik *et al.* 2001).

Los beneficios económicos que genera *Prosopis pallida* en forma de servicios ecosistémicos están valorados en más de 16.2 millones de euros al año en la región norte de Perú en forma de frutos, miel y madera (Orihuela y Albán, 2012). El fruto es usado por las comunidades rurales como alimento para el ganado y como materia prima para la producción de algarrobina, una bebida azucarada usada como edulcorante. A pesar de ello, el algarrobo es aún una especie pobremente estudiada. Según la base de datos de Web of Science, sólo se han publicado 88 artículos científicos sobre *Prosopis pallida* en los últimos 50 años (consultado el 17/11/2017). De estos artículos, la mayoría están enfocados en la morfología de la especie (Padrón y Navarro-Cerrillo 2004), la variabilidad genética (Velarde et al., 2003) y el efecto del ENSO sobre la vegetación (López et al., 2006).

Lamentablemente, hoy en día la región se enfrenta a una reducción progresiva de la producción del algarrobo en las zonas más importantes de la región debido a la sobreexplotación de la capa freática mediante pozos, la deforestación, y al incremento de las temperaturas y plagas forestales. Esto, sumado al desarrollo de la agricultura intensiva de la región, ha hecho que los pobladores rurales cambien el uso de la tierra, siendo la tala ilegal de zonas forestales el principal problema del bosque seco. Para evitar este problema, los organismos públicos duplican esfuerzos para proteger las poblaciones de algarrobo, así como ONGs y programas rurales promueven el valor ecológico

del algarrobo y las actividades de reforestación. Sin embargo, sin suficiente información básica para comprender la respuesta del algarrobo frente a factores ambientales, es difícil conseguir un resultado que perdure en el tiempo.

El clima de la región

El clima del norte de Perú está controlado por la corriente oceánica de Humboldt, y por la intensidad y frecuencia del fenómeno de El Niño. Este fenómeno es un evento climático global que provoca la inversión de las corrientes oceánicas del Pacifico Central, un incremento de las precipitaciones en la costa americana del Pacifico, y una fuerte sequía al este de Asia y Australia (Dai y Wigley, 2000). Debido a ello, en años normales (fase seca) la precipitación anual en la costa norperuana está comprendida entre 50 a 350 mm anuales, mientras que durante el ENSO (fase húmeda) puede llegar a aumentar hasta 10 veces más (Fig. 4) (Tapley y Waylen, 1990).

Durante la fase seca, la corriente circumpolar antártica fluye hacia la costa oeste de Sudamérica y conforma la corriente fría de Humboldt. La disminución de la temperatura del océano disminuye la evaporación, generando precipitaciones mínimas en la costa de Sudamérica (Rollenbeck et al., 2015). El agua caliente ecuatorial fluye por la corriente sur ecuatorial, creando un gradiente de incremento de la temperatura de este a oeste en el Pacífico Central hasta llegar a la costa de Australia, donde provoca fuertes precipitaciones y se une a la corriente Australiana del este.

Debido a la fuerte inercia térmica del Océano Pacífico, la temperatura fría del mar mantiene una fuerte correlación con la temperatura del aire (Cai et al., 2015), lo cual disminuye aún más la evaporación y las posibilidades de precipitación en la costa. La humedad generada por la evaporación del océano y por la vegetación costera es transportada hacia la costa, pero una capa de inversión térmica a 100 m de altura impide la formación de nubes. Los eventos de precipitación en la región en esta fase son puntuales y esporádicos, producto de nubes provenientes desde la Cordillera de los Andes (o desde el Océano Atlántico), o debido a la acumulación de humedad suficiente para sobrepasar la capa de inversión térmica (Rollenbeck et al., 2015) (Anexo 1).

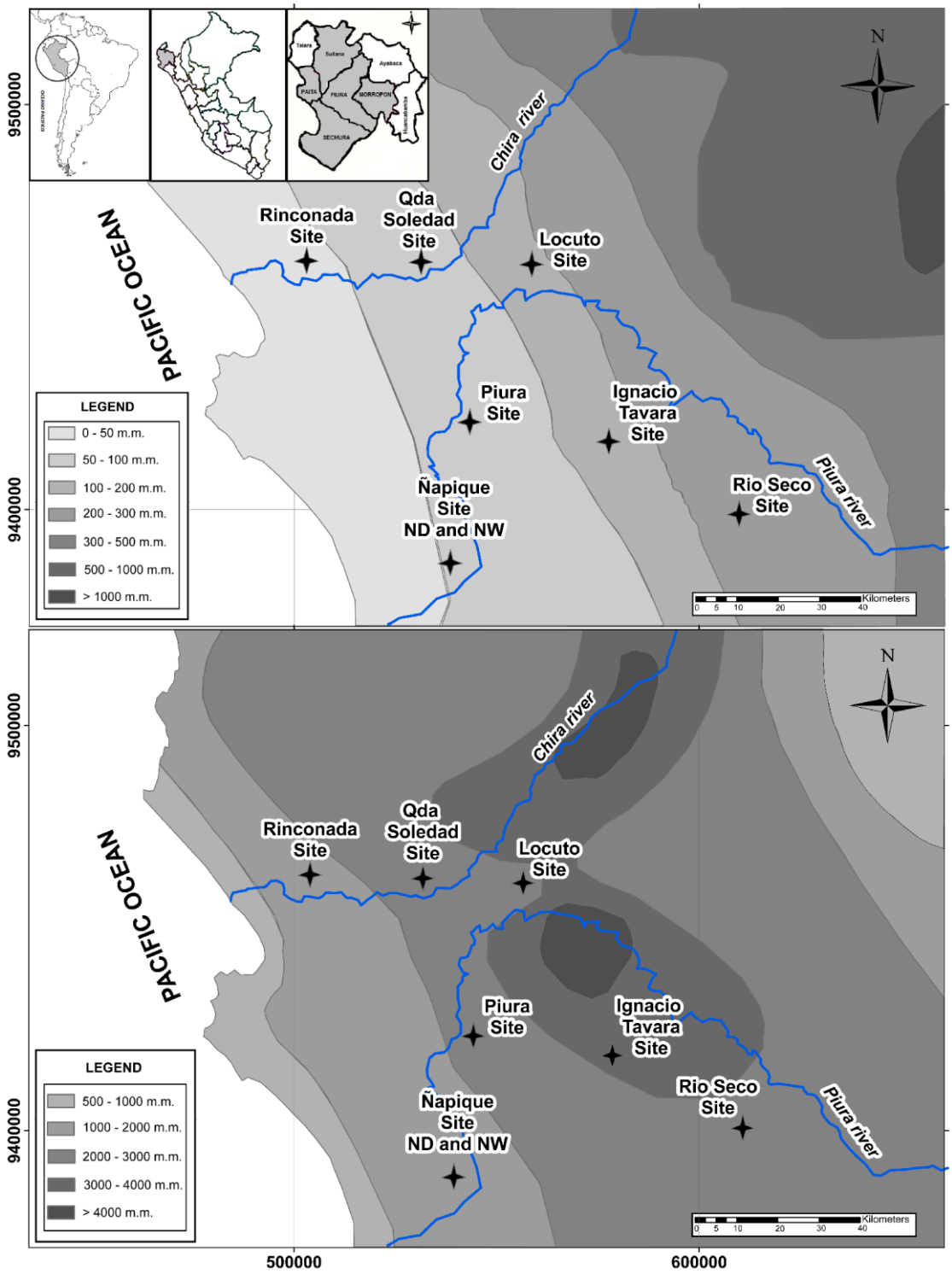

Figura 4. Precipitación media anual en la costa norte del Perú durante años normales (fase seca, No-ENSO) (ARRIBA) y durante el ENSO del año 1998 (fase húmeda) (ABAJO) (adaptado de Erdmann et al. 2008). Se indican también la localización de las poblaciones estudiadas en esta tesis.

La temperatura del aire en la región se caracteriza por mantener un ciclo anual estable, y se ajusta a una curva seno de longitud anual y amplitud de 9 grados. De esta manera es posible predecir los días más cálidos y fríos del año, que corresponden con los meses de marzo en verano y agosto en invierno (Rollenbeck et al., 2015). La estabilidad ambiental en la costa del Pacífico ha permitido la modelación del ENSO (Xue et al., 2017), de modo que actualmente existe una gran variedad de índices basados en la temperatura del mar, usados para detectar y predecir la aparición e intensidad del ENSO (Hoell y Funk, 2013; Wang et al., 2017).

Durante la fase húmeda, el gradiente de temperatura en el Pacífico central se revierte, cambiando la dirección de la corriente oceánica de oeste (Australia) a este (Perú), lo cual debilita la corriente de Humboldt y eleva la temperatura en la costa sudamericana. El aumento progresivo de la temperatura del mar suele llegar a su punto máximo en verano (diciembre a marzo), favoreciendo la evaporación e incrementando la humedad del aire, lo cual desencadena fuertes precipitaciones (Anexo 2).

Aunque los índices de temperatura del mar han demostrado su eficacia para determinar la frecuencia global del ENSO, la fase húmeda es aún un evento inestable y en algunos casos impredecible a nivel local (Griffin y Anchukaitis, 2014; McPhaden et al., 2014; Sobel, 2017). El bosque seco norperuano puede, además, tener en la región unos periodos de precipitación anómalos, cortos e intensos, llamados ENSO costeros (Rollenbeck et al., 2015; Takahashi y Martínez, 2017), que son imposibles de detectar usando los indicadores del Pacifico central.

El ciclo climático del bosque seco de algarrobo en la región de Piura está compuesto, por tanto, por una fase húmeda de corta duración (1 a 2 años) y una fase seca de larga duración (5 a 10 años, Anexo 2). La fase húmeda favorecerá la germinación de especies herbáceas y el reclutamiento de especies leñosas (Fig. 5). Esto tendrá fuertes consecuencias sobre el ciclo biológico de numerosos artrópodos, reptiles, mamíferos y aves (Catenazzi y Donnelly, 2007; Gutiérrez et al., 2007). La herbivoría, la competencia por recursos, y la dinámica de depredadores y presas tienen un papel importante sobre la composición vegetal durante este periodo (Holmgren et al., 2001). Según los modelos desarrollados por Holmgren et al. (2006), si las

precipitaciones son suficientemente intensas, la vegetación superará las condiciones adversas del desierto y la herbivoría, alcanzando un estado de "alta producción de biomasa" (Fig. 6). Al final de la fase húmeda, las temperaturas y las precipitaciones se reestablecen, la evaporación en el horizonte superficial del suelo provoca la muerte de la vegetación herbácea, y empieza la muerte paulatina de todos los organismos que componen la cadena trófica. Durante la fase seca se alcanza un estado de "baja producción de biomasa". La supervivencia a la sequía se convierte en un factor más importante que la competencia. La germinación está fuertemente limitada por la ausencia de agua superficial, mientras que el crecimiento de plantas desarrolladas y adaptadas a extraer agua de la capa freática se convierte en la principal actividad biológica del ecosistema.

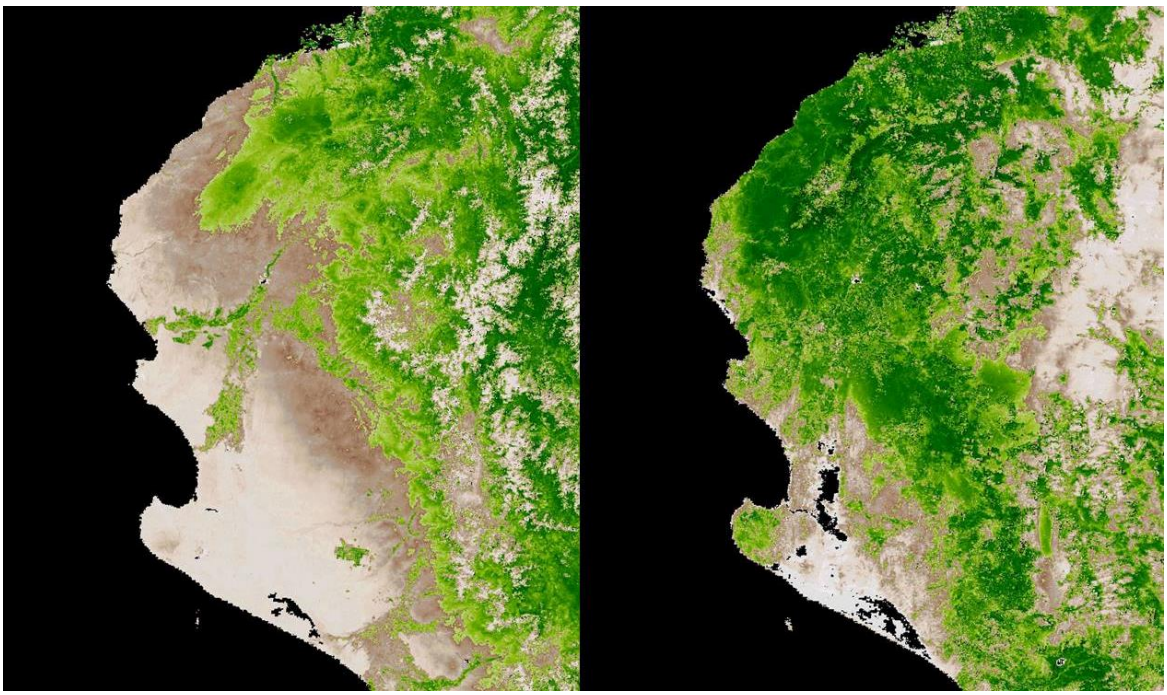

Figura 5. Imagen satelital del bosque seco de la región de Piura el 22 de diciembre del 2016 (izquierda), y el 20 de Marzo del 2017 (derecha) demostrando el impacto del ENSO de 2017 sobre la vegetación (Imagen obtenida de Google Earth).

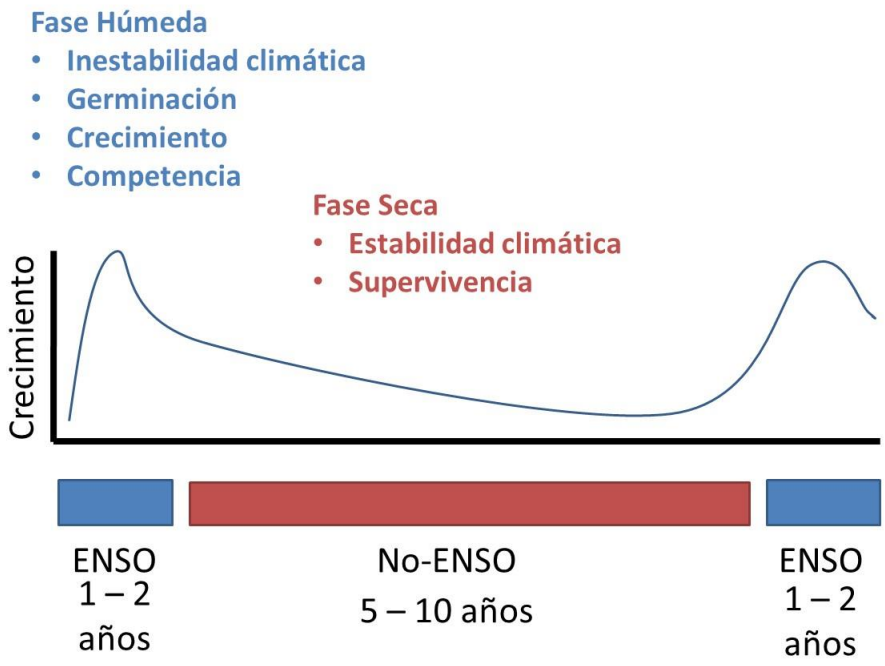

Figura 6. Distribución de la actividad biológica de las poblaciones de algarrobo durante el ciclo climatico local ENSO (El Niño Southern Oscillation).

Además de la variación temporal del clima, existe una variación espacial a lo largo de la costa, que consiste en un gradiente climático desde la costa hasta la sierra, donde la temperatura aumenta progresivamente hacia el interior al alejarse de la costa. Paralelamente, la precipitación aumenta en la misma dirección debido al efecto de las corrientes de viento que dominan la región y al transporte de las nubes desde la costa hasta la cordillera (Fig. 4). La distribución de los vientos determina la variabilidad espacial de la precipitación, mientras que el ciclo climático (ENSO) determina la variabilidad temporal de la precipitación. Estos dos factores controlan la producción de biomasa vegetal en el bosque seco (Fig. 6).

Respuesta de la vegetación a la variabilidad climática

La dendrocronología, el estudio del crecimiento a partir de la formación anual de anillos en el tronco, permite estudiar el impacto del clima sobre una especie forestal. Inicialmente, las especies tropicales fueron desestimadas en este tipo de estudios porque el clima no presenta las condiciones adecuadas para que la formación de anillos con una resolución anual (Nath et al., 2016). Sin embargo, en los últimos 30 años se han realizado numerosos estudios de

dendrocronología tropical, en especies como *Polylepis besseri* y *Cedrela angustifolia* (entre otras) que han demostrado lo contrario (Gareca et al., 2010; Paredes-Villanueva et al., 2013; Villalba, 1985). Los primeros estudios de dendrocronología en algarrobo indican que es una especie capaz de formar anillos de crecimiento (Ferrero et al., 2014), siendo sensible a la variabilidad climática y a la profundidad de la capa freática (Bogino y Jobbágy, 2011).

Los estudios realizados en algarrobo en la costa del Océano Pacífico demuestran la plasticidad de la especie frente a la variabilidad climática generada por la fase húmeda y seca. Se han observado anillos de crecimiento hasta 4 veces mayores en años de ENSO en comparación a años de no-ENSO, lo que indica que se trata de una especie sensible a la disponibilidad de agua (López et al., 2006; Rodríguez et al., 2005), y con resiliencia suficiente para soportar largos periodos secos y cortos periodos húmedos. Dado que las precipitaciones se concentran en la época de verano (Diciembre a Marzo), es de esperar que el índice de crecimiento de los anillos se relacione con las precipitaciones de verano. También se podría esperar que debido a la fuerte inercia térmica del Océano Pacífico y la relación entre la temperatura del aire y la temperatura del mar, existiera una relación positiva entre la temperatura del aire y el crecimiento radial del algarrobo.

La variabilidad espacial del clima en la región podría generar a su vez diferencias en la respuesta del crecimiento del algarrobo al ENSO. El incremento de las precipitaciones de la costa hacia el interior del continente, puede generar anillos de crecimiento de mayor tamaño en poblaciones continentales, mientras que en la costa la respuesta al ENSO sería menor. La dependencia del algarrobo de la capa freática podría jugar un papel muy importante en el crecimiento durante la fase seca, generando anillos de menor tamaño en poblaciones con menor acceso a agua subterránea (Decuyper et al., 2016). Por tanto, esperamos que la variabilidad espacio-temporal del clima provoque un efecto similar sobre la variabilidad del crecimiento en las poblaciones de algarrobo de esta región.

Plasticidad fenotípica

La plasticidad fenotípica es la capacidad de un determinado genotipo para expresar diferentes fenotipos en respuesta a diferentes condiciones

ambientales (Bradshaw, 2006), y representa el potencial de una población para cambiar frente a factores ambientales en función de su capacidad adaptativa a través de mecanismos de selección genética (Valladares et al., 2014).

Normalmente, las especies propias de zonas tropicales presentan una plasticidad fenotípica relativamente baja debido a la baja variabilidad climática anual (Valladares et al., 2014). Sin embargo, el bosque seco se presenta como una excepción única debido a la presencia del ENSO, que produce cambios significativos en la temperatura y en la precipitación cada 5 a 10 años (Wolter y Timlin, 1998). El algarrobo, al ser una especie perennifolia, debe responder y/o resistir a estos cambios. Por tanto, sus características tienen que ser suficientemente plásticas como para soportar largos periodos secos y, a la vez, responder rápidamente a la disponibilidad de agua cuando empieza la fase húmeda del ENSO. De la misma manera, la distribución espacial de las precipitaciones generadas por el ENSO cambia a lo largo del gradiente climático costero (Erdmann et al., 2008) (Fig. 4). Este aumento de la disponibilidad hídrica debería dar lugar a una importante respuesta de la vegetación, de modo que la plasticidad del algarrobo tendría que ser mayor en las zonas con mayor fluctuación climática.

Los primeros experimentos que se han realizado en *Prosopis* para evaluar su plasticidad fenotípica han estado relacionados con la respuesta a la sequía, los cuales demuestran la alta plasticidad del género *Prosopis* a la disponibilidad hídrica (López Lauenstein et al., 2012; Polley et al., 1999). En general, la escasa disponibilidad de agua genera cambios en el intercambio gaseoso, provocando el cierre estomático y la disminución de la tasa de transpiración (Delatorre et al., 2008; Quero et al., 2006). También se observan cambios morfológicos en la distribución de la biomasa como respuesta a la sequía, favoreciendo la inversión en raíz para incrementar la absorción de agua (Vilela et al., 2003). En *Prosopis pallida* podríamos esperar una respuesta similar, con modificaciones morfológicas importantes para responder al ENSO y maximizar la producción de biomasa con una alta disponibilidad de agua.

Variabilidad funcional intraespecífica

La variabilidad intraespecífica puede llegar a ser tan importante como la variabilidad interespecífica en una comunidad, especialmente en especies plásticas cuyos rasgos funcionales responden a un amplio espectro de condiciones ambientales (Albert, 2015). Las diferencias entre poblaciones pueden ser el resultado de una amplia variabilidad genética dentro de la especie (Arntz y Delph, 2001), o puede deberse a una amplia variabilidad fenotípica que permite responder a una gran variedad de condiciones con el mismo genotipo (Schneider y Meyer, 2017). La variabilidad temporal de las condiciones climáticas sugiere que el algarrobo presenta una fuerte variabilidad fenotípica que le confiere características plásticas frente a la disponibilidad de agua. Por otro lado, la variabilidad climática espacial, desde la costa hacia el interior, sugiere que también es posible encontrar una alta variabilidad intraespecífica producto de diferencias genéticas y fenotípicas entre poblaciones.

El estudio de rasgos funcionales se ha convertido en una metodología estándar para caracterizar especies y poblaciones (Reich, 2014). Los rasgos funcionales son un conjunto de características morfológicas y fisiológicas de las hojas, el tallo y la raíz, que están relacionadas con el uso de los recursos, el crecimiento, la reproducción y la supervivencia de las plantas (Díaz et al., 2015; Donovan et al., 2011). También pueden ser usados para conocer la respuesta a factores ambientales como la variabilidad climática, el pH o el contenido de nutrientes del suelo (Le Bagousse-Pinguet et al., 2015; Zhou et al., 2014). En la actualidad, los artículos que han usado rasgos funcionales para conocer la variabilidad intraespecífica del algarrobo son muy escasos (Delatorre et al., 2008; Vilela et al., 2003), por tanto, es difícil tener una idea clara de la importancia de la variabilidad funcional del algarrobo en comparación a otras especies.

La variabilidad de los rasgos funcionales frente a factores climáticos ha sido ampliamente estudiada (Albert, 2015; Wright et al., 2005). Es de esperar que un incremento en la temperatura tenga un efecto negativo en el crecimiento, mientras que la precipitación tenga un efecto positivo. Sin embargo, estas relaciones pueden cambiar según la especie y el tipo de ecosistema (Moles et al., 2014). Así, por ejemplo, en zonas áridas, donde la

precipitación es menor y más irregular, ésta puede estar menos relacionada con el funcionamiento de las plantas que la temperatura (Maestre et al., 2012). En cambio, debido a que en los bosques secos del norte de Perú existe una fuerte estabilidad de la temperatura del aire y está relacionada con la temperatura superficial del mar y la corriente de Humboldt, esperamos que esta variable se relacione significativamente con los rasgos funcionales del algarrobo especialmente en la fase seca.

Relación suelo-planta

Los suelos del Norte de Perú están compuestos por capas arenosas e inestables que son sensibles a procesos pluviales y eólicos. El suelo dominante en las áreas de distribución de los bosques de algarrobo es generalmente de textura arenosa, y presenta un bajo contenido de arcilla (1-2 %), que está relacionado con una baja capacidad de intercambio catiónico, provocando una baja disponibilidad de cationes para las raíces. Además, la textura arenosa favorece procesos de lixiviación y escorrentía durante eventos de precipitación intensos, como el ENSO (Ffolliott, 1995). Por ello, los suelos del bosque seco se consideran relativamente bajos en nutrientes, y con una alta variabilidad en sus propiedades físico-químicas relacionada con la composición vegetal (Muenchow et al., 2013).

La acumulación de metales pesados, como el arsénico, el cobre o el cadmio, son comunes en estas zonas áridas, y crean condiciones negativas para el desarrollo vegetal, limitando la biodiversidad (Haque et al., 2009; Shukla et al., 2011). Algunas especies de *Prosopis* son capaces de crecer bajo condiciones de alta toxicidad, aunque no se consideran especies hiperacumuladoras (Buendía-González et al., 2010). A esto se suma el pH básico (>8) de los suelos en la mayoría de las zonas forestales de la región (Alban et al., 2002; Pasiecznik et al., 2001). Los suelos alcalinos reducen la disponibilidad de los nutrientes del suelo, y dado que la adquisición de fósforo suele ser especialmente susceptible al pH, existe una deficiencia de nutrientes ligada a las propiedades físico-químicas del suelo más allá de su disponibilidad (Velarde et al., 2005) lo que puede provocar que algunas especies desarrollen mecanismos para reducir localmente el pH del suelo alrededor de la raíz (Lambers et al., 2015).

El estudio de la proporción de nutrientes (estequiometría) en hoja, en lugar de la concentración, proporciona información importante sobre las tasas óptimas en las cuales un nutriente puede volverse limitante debido al desbalance químico de la hoja (Ågren, 2008). Por ello, la estequiometría de nutrientes en la hoja es un indicador del estado nutricional de la planta, y está altamente influenciada por el contenido de nutrientes en el suelo. Por ejemplo, la proporción fósforo/carbono (P/C), puede modificarse en respuesta a factores externos como la herbivoría, la variabilidad climática y la fenología de la hoja (Luo et al., 2015; Schade et al., 2003; Schreeg et al., 2014). En zonas áridas, el estudio de la estequiometría de la hoja permite determinar qué elementos son más limitantes. En el bosque seco norperuano, esperamos que la composición química de la hoja en algarrobo esté relacionada con la variabilidad de las propiedades físico-químicas del suelo y la concentración de nutrientes disponibles.

El efecto de "isla de fertilidad" del algarrobo

A nivel ecológico, uno de los principales beneficios de las poblaciones de algarrobo es el incremento de la concentración de nutrientes en el suelo bajo la copa del árbol, fenómeno llamado "isla de fertilidad" (Ruiz et al., 2008), lo cual altera las condiciones del suelo, y fortalece la relación suelo-planta en zonas áridas. En bosques con presencia de especies del género *Prosopis*, el efecto de isla de fertilidad destaca por el aumento en el contenido de materia orgánica, nitrógeno, fósforo y potasio cerca de la base del árbol. Este aumento se debe principalmente a la acumulación de hojarasca, la actividad microbiana responsable de la descomposición de la materia orgánica, y la actividad de la raíz (Benata et al., 2008; Herrera-Arreola et al., 2007; Reyes-Reyes et al., 2002). Este tipo de beneficios ecológicos son difícilmente cuantificables, y normalmente se excluyen del cálculo de los servicios ecosistémicos del bosque. Sin embargo, el efecto de la isla de fertilidad es el reflejo del incremento en la fertilidad del suelo provocando la presencia del bosque, por lo cual no debería ser desestimado.

El impacto del algarrobo sobre el ecosistema puede cambiar según el lugar de estudio, las condiciones ambientales, y la especie. De modo que se han encontrado resultados positivos (Reyes-Reyes et al., 2007) y negativos (Simmons et al., 2008) sobre la disponibilidad de nutrientes en el suelo. En el

caso de los bosques secos del Norte del Perú, no se han realizados estudios orientados a determinar la importancia del algarrobo en la fertilidad del suelo, y es de esperar que la variabilidad de los factores ambientales (clima y suelo) no sólo tenga un impacto importante sobre los rasgos funcionales de las plantas, sino también tengan influencia sobre el efecto del algarrobo sobre el ecosistema.

Hipótesis y objetivos

Basado en este escenario, la **hipótesis general** de esta Tesis Doctoral es que la variabilidad de los rasgos funcionales y crecimiento de *Prosopis pallida* está relacionada con las condiciones generales del clima caracterizado por la alternancia de la fase seca y húmeda definida por el ENSO. Esta respuesta fenotípica propia de la especie, puede modificarse como consecuencia de los gradientes climáticos y edáficos locales que existen entre las poblaciones de *Prosopis*. Por tanto, diferencias locales en el régimen de las precipitaciones provocarán cambios en la respuesta del algarrobo, en la relación suelo-planta, y en el efecto del algarrobo sobre el ecosistema. Partiendo de esta hipótesis, el **objetivo general** de esta tesis doctoral ha sido conocer la variabilidad intraespecífica de rasgos funcionales y crecimiento de las principales poblaciones de algarrobo presentes en la región de Piura (Perú) en respuesta a la variabilidad espacio-temporal del clima y las características edáficas de la región.

Los objetivos específicos han sido:

1. Conocer el efecto de la variabilidad espacio-temporal del clima sobre el crecimiento del algarrobo a lo largo de un gradiente climático en la región norte de Perú mediante una aproximación dendrocronológica. El **capítulo 2** abarca este objetivo mediante el análisis dendrocronológico del crecimiento radial de 3 poblaciones de algarrobo durante los últimos 50 años.
2. Conocer la plasticidad fenotípica de las poblaciones de algarrobo de la región de Piura en relación a la disponibilidad hídrica, para determinar cómo responden diferentes rasgos funcionales frente al ENSO, así como evaluar la plasticidad de la especie a lo largo del gradiente climático regional. En el **capítulo 3** se han estudiado estos aspectos mediante un experimento de invernadero usando plántulas procedentes de semillas de 7

poblaciones de algarrobo de la región, y simulando la fase seca y la fase húmeda del ciclo climático regional.

3. Caracterizar la variabilidad intraespecífica de los rasgos funcionales de poblaciones naturales de algarrobo, y su relación con la variabilidad climática local durante la fase seca del ENSO. El **capítulo 4** abarca este objetivo mediante el estudio de 10 rasgos funcionales en 8 poblaciones de algarrobo a lo largo de un gradiente climático y geográfico entre la costa y la zona interior de la región de Piura.
4. Conocer la relación entre las características edáficas (concentración de nutrientes y pH) sobre la concentración de nutrientes en la hoja en poblaciones naturales de algarrobo. Para ello, en el **capítulo 5** se ha estudiado la variabilidad intrapoblacional de los nutrientes en el suelo y sus propiedades físico-químicas, así como la estequiometría de nutrientes de la hoja.
5. Finalmente, cuantificar el efecto del algarrobo en la formación de la "isla de fertilidad" asociada a la presencia de individuos de la especie, y su relación con las características estructurales y químicas de las hojas y el tamaño de los árboles. En el **capítulo 6** se ha estudiado la concentración de nutrientes bajo y fuera de la copa del algarrobo en diferentes poblaciones naturales de algarrobo a lo largo del gradiente climático para determinar si existe un incremento significativo de los nutrientes del suelo debido a rasgos estructurales y químicos de las hojas o bien al tamaño del árbol.

Aspectos novedosos de esta tesis

La investigación realizada en esta tesis doctoral pretende aportar varios aspectos novedosos en los estudios de bosque seco tropical, que se resumen a continuación:

1. **Dendrocronología en *Prosopis pallida***. Retomamos los estudios preliminares realizados en algarrobo (López et al., 2006), y comparamos el crecimiento con diferentes índices de temperatura del mar en el Pacífico que han ganado importancia en los últimos años en la predicción del ENSO (**capítulo 2**).

2. **Plasticidad fenotípica en especies tropicales**. Las poblaciones tropicales presentan generalmente una baja plasticidad fenotípica debido a que las condiciones ambientales son relativamente constantes (Valladares et al., 2007). Sin embargo, el impacto del ENSO en la región permite estudiar un escenario único donde la plasticidad puede llegar a ser una fuerza de selección importante (**capítulo 3**).
3. **Efecto de una alta disponibilidad hídrica en especies adaptadas a la sequía**. El algarrobo es una especie altamente resistente a la sequía (López Lauenstein et al., 2012); sin embargo, es importante estudiar también como es capaz de aprovechar la alta disponibilidad hídrica, especialmente durante la fase húmeda (**capítulo 3**).
4. **Análisis de la variabilidad intraespecífica del algarrobo**. La presencia de un gradiente climático en la región norte del Perú y la predominancia del algarrobo en el bosque seco, permite demostrar la importancia de los estudios de variabilidad intraespecífica en respuesta factores ambientales (Albert, 2015) (**capítulo 4**).
5. **Modulación de las propiedades físico-químicas del suelo**. La acumulación de ciertos elementos traza (Mn) pueden ser el resultado de modificaciones locales en el pH del suelo por parte de la raíz (Lambers et al., 2015). Debido a la escasez de nutrientes en zonas áridas, analizamos un amplio abanico de elementos en suelo y hoja que nos permitan demostrar si el algarrobo presenta esta capacidad (**capítulo 5**).
6. **Efecto de isla de fertilidad en *Prosopis pallida***. Aunque el efecto de la isla de fertilidad en el género *Prosopis* spp. ha sido documentado en el pasado (Ruiz et al., 2008), en el caso concreto de *Prosopis pallida* no había estudios hasta el momento, y la baja disponibilidad hídrica durante la fase seca podría ser un condicionante que reduzca dicho efecto sobre el ecosistema (**capítulo 6**).

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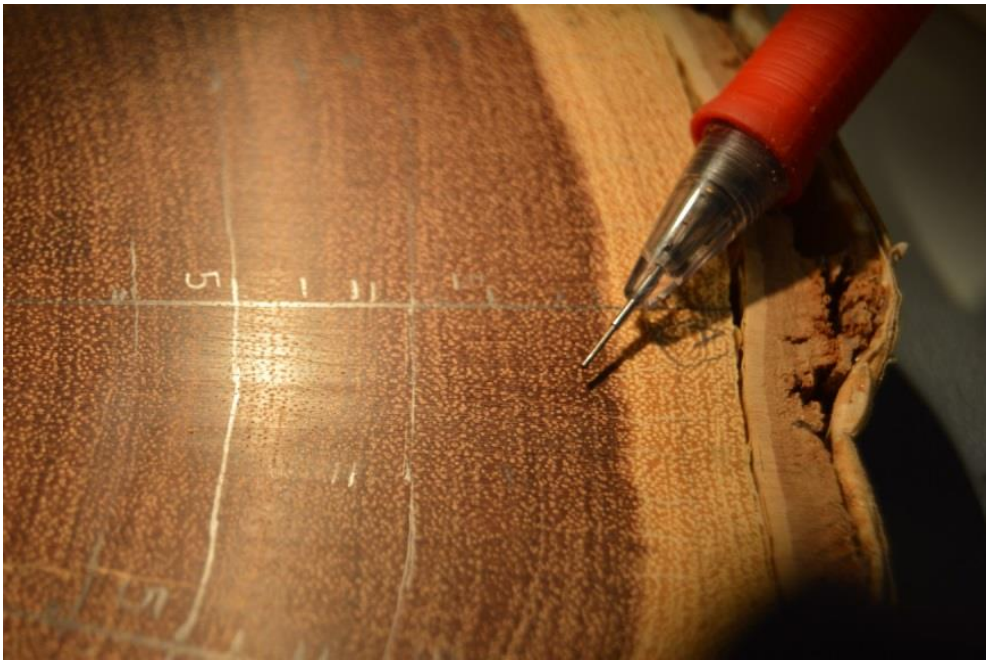

Capítulo 2

Variation of the ENSO effect on *Prosopis pallida* forests along a climatic gradient

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Abstract

Extreme rainfall events, such as the El Niño-Southern Oscillation (ENSO), are responsible to a large extent for the processes of tree establishment and tree growth in the North Peruvian dryland forest. *Prosopis pallida* (algarrobo) is the dominant species of the dryland forest on the Peruvian Pacific coast. Dendrochronological data from living populations have shown its response to climatic events. The aim of this work was to study local differences in *P. pallida* growth responses to ENSO events through dendrochronological data. To do so, three algarrobo populations within a gradient of increasing temperature and precipitation from West to East were selected. Tree-ring data were correlated with the monthly temperature and precipitation from each location and with the 3.4 and 1+2 ENSO indexes. Inland populations showed the highest correlation with the climatic conditions. The summer rainfall (January), spring temperature of the previous year, and summer temperature of the current year were significantly correlated with growth. All populations showed a significant increase in the tree-ring index during ENSO events. However, growth in no-ENSO years was also high in populations closer to the coast. Our results indicate that the proximity to the Andes Mountains, distance to the Pacific coast and distribution of algarrobo in this area make marginal inland populations more sensitive to climatic variations and ENSO events. We conclude that the *P. pallida* response to the climate in Northern Peru is the result of both strong climatic events and local conditions, which are estimated most accurately with the 1+2 ENSO index.

Keywords: 1+2 region, Tree rings, Dryland forest, Sea surface temperature, Peru

Introduction

In Northern Peru, dryland forests represent 41% of all land cover. Thousands of rural families depend directly on their ecosystem services, which are valued at 21.8 million US dollars per year (Orihuela and Albán, 2012). Continuous land degradation here has reduced vegetation cover, crop productivity, livestock numbers, and wildlife (Bonkoungou and Naimir-Fuller, 2001). As a result, and considering the present conditions, it has been stated that the North Peruvian dryland forests will disappear in the next 20 years due to timber overexploitation, overgrazing, and climate change (Orihuela and Albán, 2012).

The most important species in this ecosystem is *Prosopis pallida* (Humb. & Bonpl. ex Willd.) Kunth (hereafter referred to as algarrobo), representing 61% of all plant cover in the dryland forest. Algarrobo is a key species since birds, mammals, plants, fungi, and microbial organisms interact and survive using these trees as a nest, food source, and refuge (Biederman and Boutton, 2009; Rosi et al., 2009; Ruiz et al., 2008). The climatic conditions in this region are controlled by the Humboldt Current, which creates stable and dry conditions with minimal rainfall events. This dry phase is interrupted by the El Niño southern oscillation (ENSO), which creates a wet phase of 1-2 years of high annual rainfall and unstable climatic conditions. Plant phenology, species biodiversity, and ecological processes are shaped by this climatic cycle (Holmgren et al., 2006; López et al., 2008; Tapley and Waylen, 1990). For algarrobo, the wet phase promotes germination, growth, competition, and grazing during one year or, in some exceptional cases, two years. The dry phase promotes survival over tree establishment for an uncertain period of 4 to 8 years. Thus, the ENSO has been recognized as a trigger of long-lasting shifts in arid vegetation, switching the landscape from perennial herbs to dryland forest according to the grazing pressure (Holmgren et al., 2001) and the resistance of *Prosopis* sp. to dry conditions.

Nowadays, ENSO events have become relatively easy to study (Xue et al., 2017). A significant increase in the sea surface temperature (SST) in the Pacific Ocean, especially in the 3.4 region, is commonly used as an indicator of extreme precipitation on the Pacific coast of America (Trenberth and Stepaniak, 2001). This event is responsible for the period of greatest growth in Peruvian dryland forests, and a significant relationship between SST and

algarrobo growth is expected. However, the global and local climatic conditions could also modify plant growth. Recently, climate change has been a major concern, and a change in ENSO frequency is expected because of it. An increase in mean annual temperature might restrict plant physiologal processes, unless it is associated with an increase in mean annual precipitation. The other climatic events involved, such as the Interdecadal Pacific Oscillation or the Madden-Julian oscillation, make the forecasting of the ENSO a hard task, regardless of the increase in monitoring power (Squeo et al., 2007). For South America, the 1+2 region (0°-10°S, 90°W-80°W) of the Pacific Ocean is commonly used to determine local precipitation events and the progress of the ENSO (Vuille et al., 2015) but its relationship with algarrobo tree growth is still untested.

Dendrochronological techniques have been used to determine key variables such as tree age, annual growth, basal area increment (BAI) (Brienen et al., 2012; Schöngart, 2008), and growth-climate relationships, in order to understand forest establishment and its ecological response to climatic variability (López et al., 2013; Paredes-Villanueva et al., 2013). The earliest dendrochronological studies of *Prosopis* were made in Argentina using *P. tamarugo* Phil. and *P. flexuosa* DC. as model species (Ferrero et al., 2014; Morales et al., 2012; Villagra et al., 2005). This research defined the basic ring structure, which is related to the presence of terminal parenchyma and large-diameter vessels (Villalba et al., 2000). Based on these studies, algarrobo tree-ring data have been shown to be a good indicator of rainfall and temperature change and of how climatic variability affects forest functionality (Morales et al., 2005), with genetic variability and local climatic conditions playing an important role in the population response to rainfall events (Ramawat, 2009).

In Peru, dendrochronological studies of algarrobo have shown its positive response to ENSO events (López et al., 2006, 2005) and its potential for archeological and current climatic studies (Ghezzi and Rodríguez, 2015). Even though ENSO variability through time and space has been described in depth in the last few years, variability among populations in the response to ENSO events has not been assessed, and the role of local climatic and geographic characteristics has not been studied. In this study, we use dendrochronological techniques to evaluate the impact of ENSO events on North Peruvian populations of *P. pallida* across a climatic gradient from the

coast to inland. The results will provide information about the variability of the response to ENSO events among *P. pallida* populations, and regarding the ecological impact of this climatic anomaly on forest growth. The specific objectives of this study were (1) to analyze the tree growth variability in *P. pallida* populations and its potential for dendrochronological studies, (2) to assess the relationships among tree growth, local climatic conditions, and ENSO events, and (3) to determine whether the population response to ENSO events changes across the climatic gradient and, if so, why.

Materials and Methods

Study site

The study site is located in the dryland forests of the North Peruvian coast (5ºS), and its climatic characteristics are highly influenced by the Humboldt Current and the ENSO phenomenon. Normally, the Humboldt Current reduces the SST along the South American coast, which reduces evaporation and therefore precipitation (to below 300 mm annually) on the tropical coast of North Peru. The SST is highly correlated to the air temperature due to the thermal inertia of the Pacific Ocean, and this creates highly stable climatic conditions that closely fit a sine wave with a phase length of one year and amplitude of 7-9 °C (Rollenbeck et al., 2015). During ENSO events (wet phase), the Humboldt current weakens and the SST and air temperature rise, which increases precipitation in this region to above 2000 mm annually and creates highly unstable climatic conditions. In recent years, major ENSO events were recorded in 1953, 1958, 1964, 1972, 1982, 1987, 1992, and 1998.

Three algarrobo populations were selected in January 2015 for this study (Fig. 1; Table 1): the Ignacio Tavara (IT) community in Chulucanas, the University of Piura forest (PI) in Piura, and the Rinconada (RIN) forest in Paita. These lie along a climatic gradient, where mean annual rainfall and temperature increase from the coast to the inland areas (Table 1). Rainfall occurs in summer (between December and March), when the mean daily temperature reaches its peak, while the lowest temperature occurs in the dry season in July. The Humboldt Current reduces evaporation from the sea, and the wind field removes most of the dew. Therefore, there is no significant presence of fog in these dryland ecosystems (Rollenbeck et al., 2015). The IT

and RIN populations have grown naturally under human management to improve pod production, while the PI population has grown as part of a reforestation program with a similar management strategy. In all cases, forest management has consisted only of scheduled pruning, without the use of fertilizers or pest control strategies. Despite this, the populations differ morphologically, functionally, and structurally, and there is high genetic variability among them (Palacios et al., 2011). Regarding the soil texture, the sand content exceeds 98% in all three locations, and the soil pH is slightly acid (6.45-6.69).

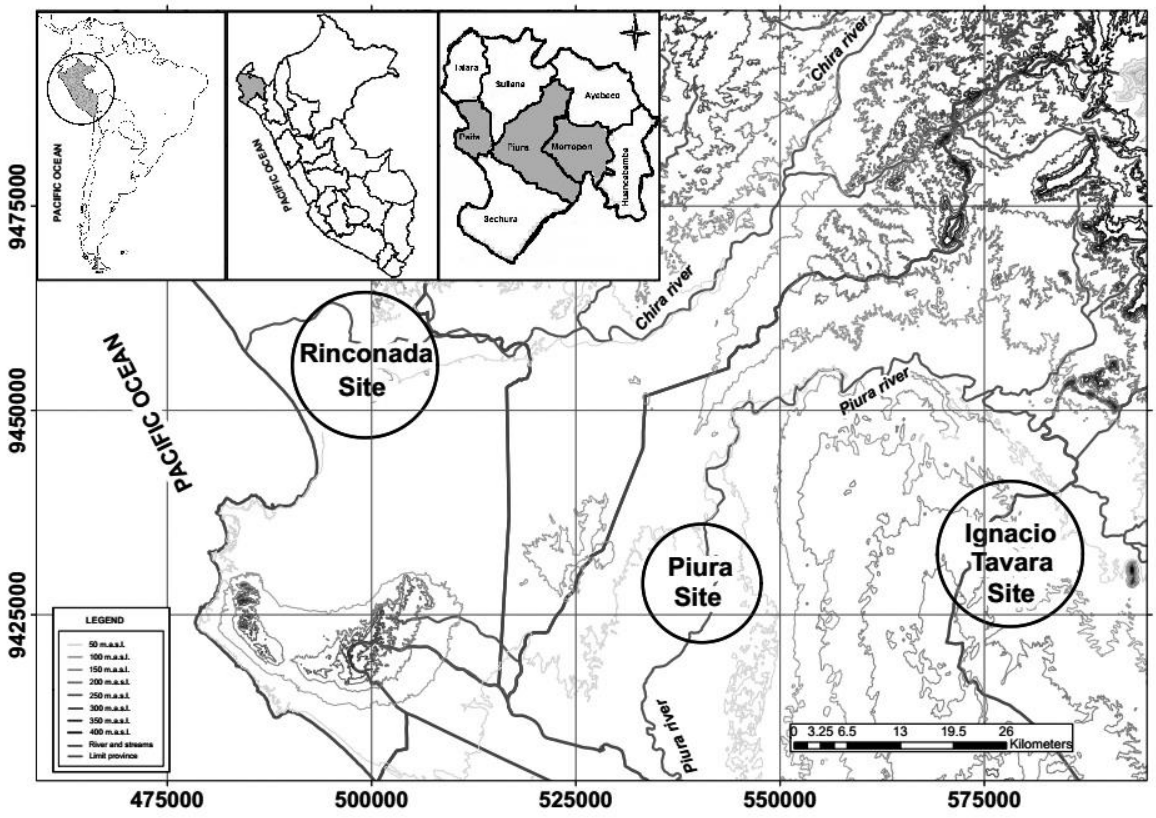

Figure 1. Geographic location of the populations studied in North Peru.

Table 1. Geographical, topographical and morphological characteristics of three *P. pallida* populations

Variable	Ignacio Tavara	Piura	Rinconada
Latitude	5°12'22.66"S	5°10'43.28"S	4°54'19.13"S
Longitude	80°11'32.46"O	80°38'7.46"O	81° 0'59.88"O
Altitud (m a.s.l.)	153	72	93
Distance from the sea (km)	108.83	59.24	13.72
Annual Rainfall (mm)	208	48	52
Mean Annual Temperature (C)	24.8	23.9	23.4
Tree DAHC (m)	0.32±0.05	0.28±0.04	0.30±0.5
Tree Height (m)	8.8±0.4	9.1±0.7	11.1±0.5
Age (years)	44	50	51
Soil Texture	Sandy	Sandy	Sandy
Soil pH	6.45±0.1	6.69±0.04	6.51±0.07
Groundwater deep (m)	50	10	5

Field sampling and sample preparation

Ten cross-sections per population were collected, with the approval of SERFOR and the nearby rural communities. The relatively small number of tree samples analyzed in this study might be seen as a limitation. However, the North Peruvian dryland forest is a scarce and endangered ecosystem. Thus, tree logging, especially for older trees, is forbidden. At each site, care was taken to select trees more than 30 years old, growing under similar microsite and competition conditions, and located at least 20 m apart from each other, across a rectangular area of 1 ha. Sections were taken at breast height (1.30 m) specifically for this study. Cross-section samples were air-dried and polished with sandpaper of different intensity, following the grain standards of the Federation of European producers of abrasives (https://www.fepa-abrasives.com/), from P24 to P2500, until the terminal parenchyma was clearly visible under a binocular microscope. Up to two radii were selected in each cross-section. The tree-ring width was measured digitally in each radius within each section, for all the selected trees. Due to the irregular radial growth of *P. pallida*, tree rings were analyzed across the entire disk to detect false or double rings. The correlation coefficient among samples was also considered during the elimination and addition, respectively, of double and

missing rings. The ring width measurement and crossdating were performed using CooRecorder and CDendro 7.8 (2014 - Cybis Elektronik & data AB).

An annual tree-ring width chronology was built for each site. All tree-ring series were prewhitened and biweighted to remove variation not related to climatic factors during the standardization process, thereby allowing determination of the correlation between series within each population. To compare population growth and the impact of ENSO events, the mean BAI was calculated using tree-ring data, with the formula $BAI = \pi (R^2_t - R^2_{t-1})$ (mm^2 $year^{-1}$), where R is the radius of the tree and t is the year of tree-ring formation, for each population.

To build the correlation chronology of each population, individual tree-ring width series were double detrended, first using a negative exponential curve and then by fitting a cubic smoothing spline with a 50% frequency response. The mean sensitivity was also calculated, to study the year-to-year variability of the tree rings. Principal component analysis (PCA) was computed with all individual residual series for successive 20-year periods lagged one year, to study the source of growth variation. Correlations between the samples, BAI, correlation chronology, mean sensitivity values, and PCA were calculated using the "dplR" package of R software (Bunn, 2010, 2008).

Dendrochronological statistics were calculated for the common interval 1990-2010, to compare growth features among the study sites (Fritts, 1976). The mean and standard deviation (SD) of the raw tree-ring width data were calculated to compare growth among populations and with other *Prosopis* species. The first-order autocorrelation of the tree-ring width raw data (AR1) was calculated to determine the degree of independence of the tree-ring growth series from each other through time. The mean sensitivity (MS) of the residual series was calculated to study the year-to-year tree ring variability. The mean correlation of the common period (MCCP) was calculated to show the consistency of the dendrochronological results. The expressed population signal (EPS) of the residual width series was calculated to determine the common relationship with external factors. Finally, the percentage of the variance explained by the first principal component (PC1) was calculated to determine the main source of variation.

Climate data and climate-growth relationship

To analyze climatic trends at a regional scale and quantify climate-growth relationships, we used monthly climatic data (mean temperatures and total precipitation) from the CRU TS 3.1 dataset for the period 1963-2014, produced by the Climate Research Unit (http://www.cru.uea.ac.uk/). This dataset corresponds to the interpolated data of instrumental records recorded by a dense network of local meteorological stations, which have been subjected to homogeneity tests and relative adjustments, and finally gridded onto a 0.5º network (Mitchell and Jones, 2005). Furthermore, ENSO indexes from the 3.4 (5°N-5°S, 170°W-120°W) and 1+2 (0°-10°S, 90°W-80°W) regions from the NOAA organization (http://www.noaa.gov/) - which record climatic fluctuations and the mean SST in the Pacific - were considered to study the ENSO influence on regional precipitation patterns and tree growth (Trenberth and Stepaniak, 2001). Monthly SST indexes from the 1+2 region were correlated with the mean chronology of each population from August of the previous year to July of the current year. Seasonal SST means were calculated for the Niño 3.4 and 1+2 regions and then correlated with the tree-ring width and the first axis of variation of the PCA for each population. Correlations between the climate data and each population chronology were calculated using the "dcc" function of the "treeclim" package of R software (R Development Core Team, 2013).

Results

Tree growth

The *P. pallida* populations showed high tree-growth variability, with a low tree-ring index under average climatic conditions (dry phase) that was three-fold higher in ENSO years (wet phase). This growth pattern was consistent among populations, with a significant response to ENSO events over time, but the response varied between populations (Fig. 2). Thus, the mean tree-ring width was greater (2.5 mm) during ENSO events than in normal years (0.8 mm) at IT, where growth seems to be more ENSO-dependent (Fig. 3). Meanwhile, the mean tree-ring width during ENSO events (1.8 mm) was similar to that in normal years (1.2 mm) at RIN. In the PCA, a high amount of the variance was explained in the first axis, for all populations

(Table 2). Despite this, there was no common trend in PC1 among the populations (Fig. 4), suggesting that they have different sources of variation. The mean sensitivity was high but within the range of *P. pallida* data reported previously. Peaks of the mean sensitivity were present in ENSO years, but did not appear consistently among populations, indicating again a differential response in each site (Fig. 5).

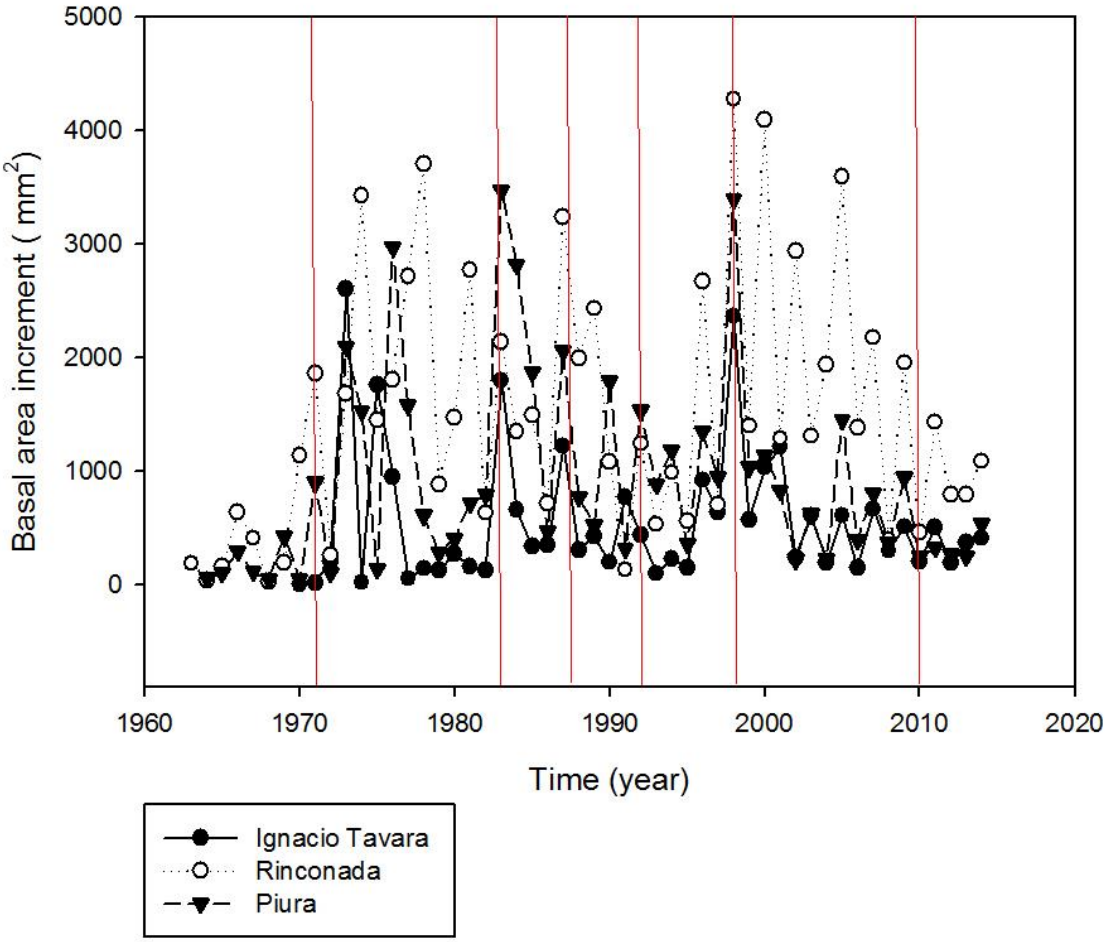

Figure 2. Basal area increment (mm^2) for the inland and coastal populations over time. Vertical line indicates recorded ENSO events.

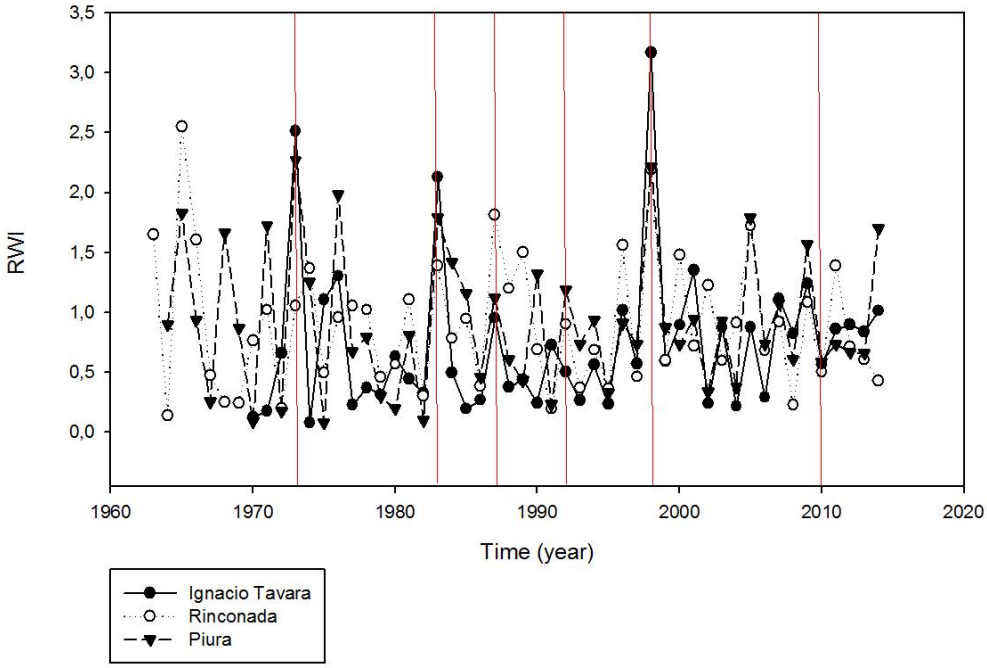

Figure 3. Chronology of the tree-ring width index for *P. pallida* populations. The trend of this index is given by the Loess smoothing curve. Vertical lines indicate recorded ENSO events.

Table 2. Characteristics of the tree-ring chronologies for the common period. SD, standard deviation; MSx, mean sensitivity of the residual ring width series; MCCP, mean correlation of the common period; EPS, population signal of the residual series; PCA1, the first axis of the principal component analysis; PCA2, the second axis of the principal component analysis.

Variables	Ignacio Tavara	Piura	Rinconada
Nº of Tree (radii)	10 (14)	11 (11)	10 (10)
Tree-ring width (mm)	3.13	3.45	3.95
SD (mm)	7.20	4.79	5.45
AC1	0.07	0.39	0.33
MS_x	0.98	0.9	0.91
MCCP	0.44	0.49	0.34
EPS	0.81	0.86	0.84
PCA1	0.50	0.44	0.46
PCA2	0.14	0.13	0.12

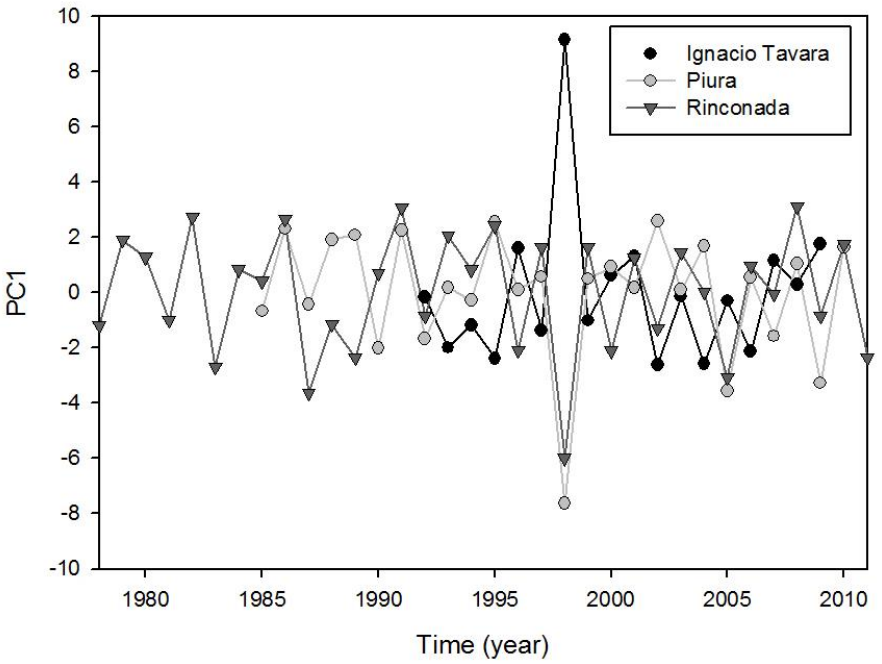

Figure 4. Temporal trend in the variance explained by the first principal component analysis for Rinconada (34 year subinterval), Piura (26 years subinterval) and Ignacio Tavara (17 years subinterval).

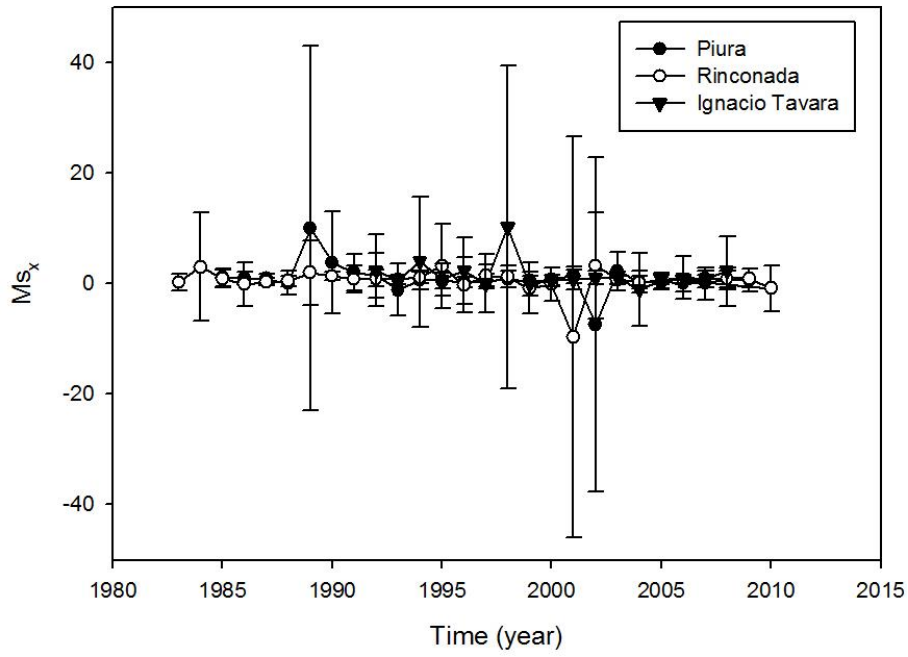

Figure 5. Temporal trend in the mean sensitivity and its standard deviation using a subinterval of 34 years for Rinconada, 26 years for Piura. and 17 years for Ignacio Tavara.

Interaction between growth and local climate

The tree-growth index was positively correlated with the precipitation in January of the growth year, the highest monthly precipitation of every year, and the precipitation during the ENSO rainfalls. The correlation coefficient was higher at IT ($r = 0.67$) than at PI ($r = 0.40$), and was nonsignificant at RIN (Fig. 6), showing the importance of the climatic gradient from the coast to inland areas and the differential response of each population to the environmental conditions. Similarly, the tree-growth index was positively correlated with the mean monthly spring temperature of the previous year (October, $r = 0.50$) and the summer temperature of the current year (January, $r = 0.32$; February, $r = 0.22$; and March, $r = 0.21$) at IT, while at PI it showed less significant relationships with the spring temperature of the previous year (October, $r = 0.39$; December, $r = 0.32$). There were no significant correlations in the case of RIN (Fig. 6).

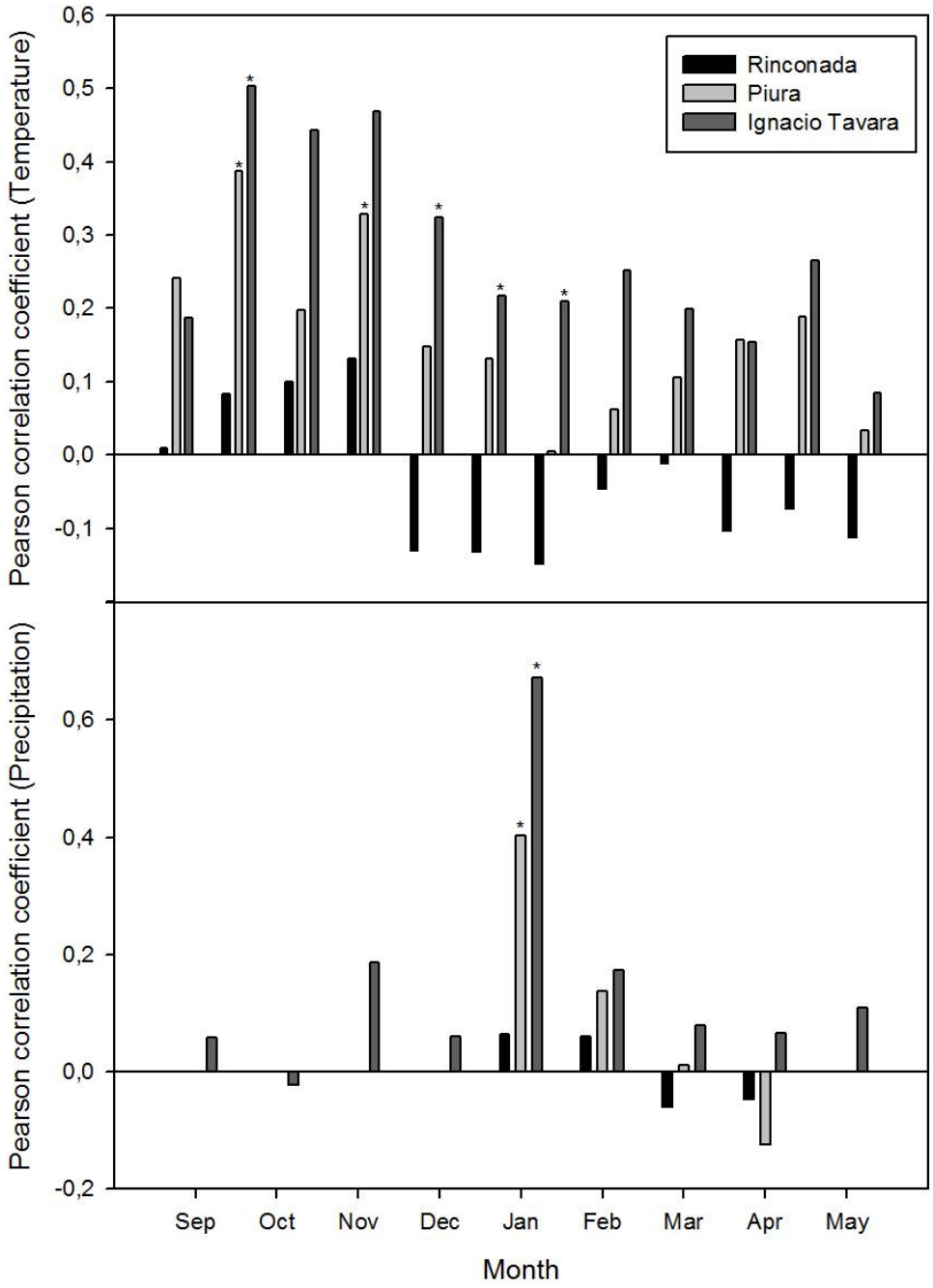

Figure 6. Correlations of monthly total precipitation and monthly mean temperature with tree-ring index during the growing season of *P. pallida*.* $p<0.05$.

Population response to ENSO events

At IT, the tree-growth index was significantly correlated with the mean sea temperature index (1+2 ENSO) in the spring of the previous year (r = 0.53) and in the summer of the current year (r = 0.57). For IT, the first axis of the PCA was also highly correlated with the sea temperature during these periods; however, this relationship was not significant (r = 0.79 and r = 0.71, respectively). Populations PI and RIN showed no significant correlation with the SST in the 1+2 or 3.4 ENSO region in any season (Table 3).

Table 3. Pearson correlation coefficient between PC1 and the tree growth index of each population, and the mean sea surface temperature indexes from the Niño 1+2 and Niño 3.4 geographic areas.

ENSO sea surface temperature indexes		**Principal component analysis (PC1)**			**Tree growth index**		
		IT	**PI**	**RIN**	**IT**	**PI**	**RIN**
Niño 1+2	Winter (t^{-1}) (J-A-S)	0.79	-0.68	-0.33	**0.53***	0.36	0.18
	Spring (t^{-1}) (O-N-D)	0.70	-0.64	-0.45	0.58	0.37	0.26
	Summer (t) (E-F-M)	0.71	-0.55	-0.47	**0.67***	0.31	0.32
	Autumn (t) (A-M-J)	0.44	-0.48	-0.34	0.43	0.29	0.24
	Winter (t) (J-A-S)	0.04	-0.15	-0.04	0.21	0.17	0.02
Niño 3.4	Winter (t^{-1}) (J-A-S)	0.51	-0.43	-0.29	0.41	0.19	0.07
	Spring (t^{-1}) (O-N-D)	0.36	-0.37	-0.25	0.37	0.19	0.05
	Summer (t) (E-F-M)	0.31	-0.36	-0.25	0.36	0.15	0.09
	Autumn (t) (A-M-J)	-0.05	-0.28	-0.07	0.15	0.07	0.03
	Winter (t) (J-A-S)	-0.45	0.06	0.19	-0.18	-0.09	-0.01

The monthly correlation between the tree-growth index and SST index (1+2 ENSO) was significant for IT in August (r = 0.55), September (r =0.56), February (r = 0.61), and March (r = 0.53). Similarly, the PI tree-growth index and sea temperature in August (r = 0.38) and September (r = 0.40) were positively correlated, while the RIN tree-growth index showed no correlation with sea temperature in any month (Fig. 7).

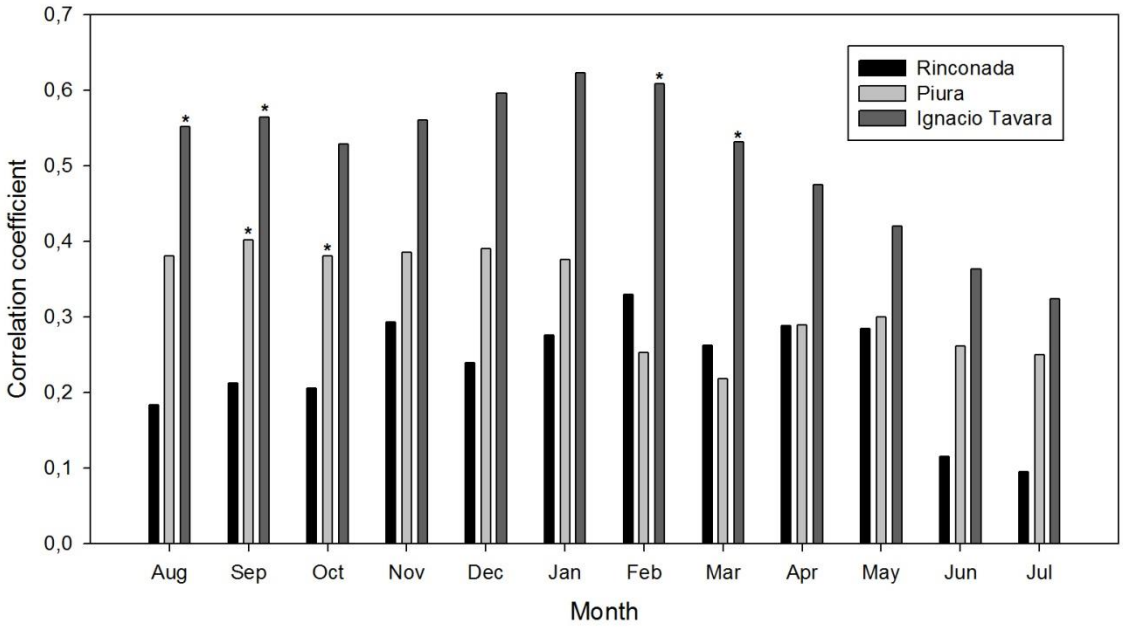

Figure 7. Correlations of mean sea temperature in the Niño 1+2 region with tree-ring index of *P. pallida* in each population.* $p<0.05$.

Discussion

Our results show that algarrobo has a common dendrochronological signal that is highly correlated with the local climatic conditions and the SST in the Niño 1+2 region. However, this relationship was not consistent among populations, suggesting that the heterogeneous distribution of precipitation along the North Peruvian coast can hinder the effects of the ENSO phenomenon.

Prosopis pallida tree growth

Despite what previous dendrochronological studies have suggested (Speer, 2010; Towner, 2002), tropical species are able to provide good dendrochronological results. The dendrochronological characteristics of each population were similar to those found in previous studies (López et al., 2006, 2005). The mean sensitivity values were quite high, even in comparison with *Prosopis ferox* (Morales et al., 2001) or *Prosopis caldenia* (Bogino and Jobbágy, 2011), but were similar to those reported by Lopez (2006) and Rodriguez (2005). Even though this suggests that variation with time is independent of external factors, it has been proposed that sensitivity values are

inefficient estimators of the coefficient of variation (Bunn et al., 2013). Our results also show low autocorrelation values and relatively small standard deviations, considering the impact of ENSO events (López et al., 2008), which are also considered good indicators of sensitivity in dendrochronological sequences. The MCCP was relatively low, but in line with other *Prosopis* studies (Bogino and Jobbágy, 2011; López et al., 2006; Morales et al., 2001; Rodríguez et al., 2005) and tropical dendrochronological studies (Ferrero et al., 2014; Gareca et al., 2010). The relatively small number of samples did not reduce the significance of our results, considering that similar AC1 and sensitivity values were found by Lopez (2005) for *P. pallida*. Therefore, the *P. pallida* populations show a common dendrochronological signal, and it reaches the standard of other tropical dendrochronological studies. Its potential for the study of ENSO variation through time and its effect on plant ecosystems makes it the right candidate for dendrochronology on the South Pacific coast.

On the South American Pacific coast, air temperature and SST are closely related, and they remain low during the dry season due to the Humboldt Current. Sea breezes reduce the mean temperature at coastal sites and create a gradient of temperature from the coast to inland sites. The wind field flows east and reduces cloud formation at coastal sites, allowing higher precipitation at inland sites. This creates a climatic gradient between the coast and the inland areas in which temperature and precipitation are positively correlated. The SST increases in summer, along with the air temperature, and rainfall events occur (a total of 50-250 mm per year), with fewer on the coast than in inland territories. Our results confirm the importance of summer rainfall for algarrobo annual growth but also show that mean monthly temperature could be an indicator of growth at inland sites. These precipitation events are enough to ensure algarrobo establishment, by promoting fast root growth and allowing water extraction from deeper soil layers (Squeo et al., 2007). For *P. pallida* dryland forest, the mean temperature could be an indicator of positive climatic conditions for growth - stimulating the beginning of the growing season and enhancing tree-ring width - as our results show a significant, positive effect of higher mean monthly temperatures on growth for IT and PI.

Above a certain threshold, a rise in temperature should have a negative effect on tree-ring growth, especially during the dry season. IPCC reports suggest that a temperature increase will be linked to an increase in rainfall events and in ENSO frequency, in a long-term future (Bates et al., 2008; Wang et al., 2017). However, this has not been the case yet. The BAI and tree-growth index have shown minimal increases in recent years. This confirms that the climatic conditions along the North Peruvian Pacific coast have become more limiting to growth in the last decade, a time characterized by long periods of drought, an increase in mean temperature, and limited rainfall events (Caycho et al., 2016; Caycho and Lavado, 2014). Similar changes have been registered for other forests of the Pacific coast. In the North America, a 4-year drought on the Pacific coast has affected the Californian Mediterranean forest, and represents an exceptionally severe drought in the context of the last millennium (Griffin and Anchukaitis, 2014). Weakening of the East Asian summer monsoon has caused droughts in Northern China (Cai et al., 2015). The source of these long-term arid conditions is a significant increase in SST. The continuous warming of the Pacific Ocean since the 1950s has been detected (Levitus et al., 2000), alongside an increase in the SST in the Indian and Southern Oceans (Gille, 2002). In Peru, the effect of the increasing SST has been a progressive increase in the temperature in the Andes Mountains during the last 50 years, with subsequent increases in the air temperature in inland and higher-elevation locations (Vuille et al., 2015). Thus, our BAI and tree-growth index results show that the warming of the Pacific Ocean has started to threaten algarrobo growth and survival, especially for inland populations such as IT.

Differences in growth-climate relationships among populations

The correlations between the tree-growth index and climate differed among populations. At IT, tree growth was highly correlated with January rainfall from the current year; a lesser but significant correlation with January rainfall from the current year was found for PI, while there was no correlation between monthly rainfall and tree growth for RIN. The difference in plant response to rainfall events among populations could be mostly related to the total annual precipitation, which is 4-fold higher at IT than at RIN or PI. This suggests that the annual precipitation events at RIN and PI are not intense

enough to generate a physiological response and these populations probably rely on phreatic layers of underground water (Ramawat, 2009), which occur at less than 5 m depth for RIN and at 10 m for PI (Alvarez et al., 2002, 2004). This is also the case for *Prosopis flexuosa* in Argentina, where the climate-growth relationships also depend on the groundwater depth (Bogino and Jobbágy, 2011). Thus, lowland populations, similar to RIN and PI, are less responsive to rainfall and are influenced more by other growth-control factors like temperature. Climatic conditions play a more important role in *Prosopis* growth in high-altitude populations, for which precipitation in January is the main source of available water and underground water is less accessible because it is located at a depth of 50 m (Alvarez et al., 2002).

Alongside the depth of the underground water, differences among sites in the rate of herbivory could explain growth variability among populations. Precipitation events may increase insect outbreaks and reduce growth, counteracting the effect of increased water availability (Koprowski and Duncker, 2012). During the ENSO wet phase, plant growth can shift into a high biomass state and overcome herbivory (Gutiérrez et al., 2007). After that, low precipitation during the ENSO dry phase at coastal sites may reduce the probability of insect outbreak, while relatively higher rainfall at inland sites may promote insect herbivory. Therefore, higher herbivory levels associated with rainfall events and high temperature in the dry season may modify plant growth more strongly at inland than at coastal sites. Thus, the IT population will likely need stronger rain pulses for its plants to be able to escape the negative effect of insect herbivory and show positive growth during the ENSO dry phase (Scheffer et al., 2008).

The role of ENSO events in Prosopis pallida radial growth variability

The relationships between the SST and major climatic phenomena - such as the ENSO, the interdecadal Pacific oscillation (IPO), or the Madden-Julian oscillation - indicate that the Pacific Ocean has a great heat capacity and thermal inertia, being a major contributor to the long-term climatic conditions (Cai et al., 2015). The SST has been remarkably useful in the study of the intensity and frequency of the ENSO; specifically, in the 3.4 region of the Pacific Ocean, where the first signs of water warming up and flowing from West to East can be recorded and used as an indicator of the ENSO. Thus, the

forecasting and monitoring of ENSO events have become relatively easy (Xue et al., 2017); but, regardless of the predictive power of these indexes, a rise in the SST in the Pacific Ocean does not necessarily have an impact on plant growth. The ENSO events in 1975, 2005, 2010, and 2016 did not have a significant effect on summer precipitation (Caycho et al., 2016; McPhaden et al., 2014). Accordingly, our results show that the SST of the 3.4 region does not seem to have a significant correlation with *P. pallida* tree growth. Instead, variation in the SST of the 1+2 region, which is geographically closer, seems to be a more reliable indicator of precipitation events and is probably responsible for changes in local conditions. This result sets the limits of the potential dendroarchaeological use of *P. pallida*, suggesting it may not be a good indicator of SST variation in the central Pacific.

Moreover, only the IT population exhibited a high correlation with the SST in the 1+2 region of the Pacific Ocean. Other *P. pallida* populations, such as RIN and PI, clearly benefit from ENSO events but their growth is not limited to extreme rainfall events. Three factors probably contribute to the differential response of the IT population to rainfall events. (1) Close proximity to the Pacific coast increases humidity and reduces air temperature, producing climatic conditions favorable for growth even with minimal rainfall. This allows growth in the RIN and PI populations during the dry phase of the no-ENSO years, while inland populations, like IT, have restricted growth because they are more susceptible to higher temperatures. (2) The increase in air temperature near the Andes Mountains should also play a role, because the climatic conditions in this area are highly correlated with the SST. Thus, higher temperatures at inland and higher-elevation sites, like IT, are the result of a strong vertical stratification of temperature in the atmosphere, which has been described along the Chilean and Peruvian coasts (Vuille et al., 2015). Finally, (3) it is possible that these differences are due to the regional distribution of algarrobo. Marginal populations usually have greater sensitivity to climate and show a strong response to both temperature and precipitation (Cook and Kalriukstis, 1990; de Ridder et al., 2013). The IT population is located farther from the coast and can be considered a marginal population in the *P. pallida* regional distribution. Therefore, it may be more sensitive to climate (temperature and precipitation) variation.

Based on these results, the search for algarrobo timber remains in archeological studies could provide enough dendrochronological data to reconstruct ENSO events from approximately 2000 years ago. Algarrobo could also be used to study the Medieval Climate Anomaly (MCA), and whether it was a global event or a regional North Atlantic phenomenon. Recent results indicate that MCA and SST data are more likely to be related due to the century-scale variability. The presence of medieval log remains from the Inca periods, alongside seashell and coral remains (Rustic et al., 2015), could aid the elucidation of whether the MCA event had a significant impact in the South Pacific Ocean and whether it interacted with ENSO events.

Conclusion

Our results show that *P. pallida* populations on the North Peruvian coast are a good candidate for dendrochronological reconstructions, especially for the detection of current and historical strong climatic events such as the ENSO. Due to the wind field and Humboldt Current dynamic, coastal sites received lower precipitation than inland sites. Despite this, the growth of inland populations showed a closer relationship with summer precipitation and temperature than that of coastal populations. The climatic dependency of inland populations is the result of a deeper groundwater level and high temperatures that create stressful conditions for growth. Similarly, these populations showed higher sensitivity to ENSO events and Ocean surface temperature indicators, such as the 1+2 ENSO index, due to their proximity to the Andes Mountains.

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Capítulo 3

Variability in growth, biomass allocation and phenotypic plasticity to the water availability response in seven *Prosopis pallida* populations

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Abstract

The North Peruvian dryland forests face long drought periods with limited precipitations every year, which may promote adaptive mechanisms to cope with low water availability. However, the impact of the El Niño South Oscillation (ENSO) in these forests provides a unique set of conditions with high water availability that increase water consumption and plant growth. We studied the performance of *Prosopis pallida* seedlings (an abundant tree species in these forests) from different populations along an environmental gradient (mainly rainfall and temperature). We want to know if the response to water availability in growth and biomass allocation differ between the different populations. We expect that phenotypic plasticity plays an important role to overcome drought conditions and take advantage of extreme rainfall events in this species. For that, we grew seedlings from seven *P. pallida* populations in a greenhouse experiment with low and high water availability (40 and 80% field capacity, respectively) during two months. Under high water availability, plant biomass was positively correlated to evapotranspiration and root mass allocation, and negatively correlated to leaf mass per area (LMA), while wood density (WD) was negatively correlated to water potential under low water availability. Relative distance plasticity index (RDPI) showed that populations respond differently to water availability. Evapotranspiration, mean annual temperature and rainfall from the place of population origin were correlated with the phenotypic plasticity of a few traits (instantaneous water use efficiency, plant height and water use efficiency), showing that it was reduced under harsh climate conditions. In summary, root mass allocation, water transport, and leaf structure play an important role in plant growth under extreme rainfall events. Overall, variation in phenotypic plasticity was not related to climatic factors.

Abbreviations

PH: Plant height (cm), PB: Plant biomass (g), LMR: Leaf mass ratio, SMR: Stem mass ratio, RMR: Root mass ratio, TLA/Root: Total leaf area/Root biomass (cm^2 g^{-1}), ET: Evapotranspiration (L), WP: Water potential (MPa), WUE: Water use efficiency (L g^{-1}), LMA: Leaf mass per area (g m^{-2}), WD:

Wood density (g m^{-3}), A_{mass}: Net photosynthetic rate per leaf dry mass (nmol CO_2 g^{-1} s^{-1}), g_s: stomatal conductance mmol H_2O m^{-2} s^{-1}) and WUEi: Instantaneous water use efficiency (A/g_s).

Keywords: drought; LMA; mean annual temperature; water use efficiency; wood density, Peru

Introduction

The differences in plant resource-use strategies have been mainly characterized by the trait differences between distint species (Díaz et al., 2015; Quero et al., 2008; Wright et al., 2004). However, in recent years both the intraspecific trait variability and their phenotypic plasticity have been also used to understand plant differences and the different response to environmental factors (Nicotra et al., 2010; Vilela and González-Paleo, 2015). Phenotypic plasticity is defined as the capacity of a given genotype to render different phenotypic response under different environmental conditions (Valladares et al., 2006). The phenotypic plasticity represents the potential of plants to adapt under new conditions as a function of local adaptation through genetic selection mechanisms (Valladares et al., 2014).

Despite the relative low plasticity expected in tropical ecosystems with low annual climatic variation (Valladares et al., 2014), North Peruvian forests present itself as a unique exception due to the periodic presence of El Niño Southern Oscillation (ENSO) which increase the temperature up to 2 °C and the precipitation up to 2000 mm during the summer (Wolter and Timlin, 1998). High water availability in this dryland ecosystem increase leaf and stem growth, which will be associated to a high response of biomass allocation (Vilela et al., 2003). Also, the increase in water availability will support a high response of the plant gas exchange (Delatorre et al., 2008). Under these environmental conditions (high water availability and a slight increase in temperature), the risk of cavitation in the xylem should be reduced, allowing *P. pallida* to produce large vessels in the stem, which may decrease stem density.

After the ENSO, new and very different environmental conditions are established, having a long dry phase (5-7 years) with a strong climatic stability and a short rainy season from February to March (50 to 250 mm) (Rollenbeck et al., 2015). Under these low water availability conditions, stomatal closure is the most common physiological response to cope with water stress in many species (Bongers et al., 2017; Delatorre et al., 2008; Quero et al., 2006). Water use regulation is favored, and then selection for drought tolerance may favor lower gas exchange rates that result in a higher water use efficiency (Arntz and Delph, 2001). A significant increase of root development has been described as a plant response to water stress allowing to explore underground soil water under drought conditions (Guevara et al., 2010; Poorter et al., 2016). Thus, plants in this region could be adapted to faced ENSO events as disturbance regimes that change water availability, food webs, and herbivory dynamics (Holmgren et al., 2006). Also, structural and physiological adjustments are required to survive under long droughts, and to grow and reproduce after extreme precipitation events, suggesting that a strong phenotypic plasticity in plants should be beneficial in this region (Loreti and Oesterheld, 1996).

Algarrobo (*Prosopis pallida* H. et Bonpl. ex Willd. H.B.K.) is a leguminous tree which covers large areas of the dryland forest ecosystems in North Peru and has faced ENSO and no-ENSO precipitation regimes through its history. Based on dendrochronological records, ENSO events play a significant role in *P. pallida* growth and establishment (López et al., 2006, Salazar et al. Capítulo 2). Thus, phenotypic plasticity to water availability should allow *P. pallida* to shift from a survival strategy to a growth strategy. Therefore, these disruptive environmental changes will favor high phenotypic plasticity (Nicotra et al., 2010). However, under prolonged stable conditions, the presence of a high plasticity become an unnecessary cost (Valladares et al., 2007). When plasticity is no longer required, trait variability should be reduced and the most suitable phenotype should be selected for the current conditions. Thus, the reduction of plasticity has been related to specialization events (Pohlman et al., 2005). In our case of study, *P. pallida* populations are located in an increasing climatic gradient from west to east. Most of the time, these populations have to face no-ENSO conditions with limited rainfall

events. Coastal populations face stable conditions with lower rainfall and temperature than inland populations. During ENSO years, rainfall periods will increase in all populations; however, differences between populations across this gradient increase exponentially (Erdmann et al., 2008). Thus, our hypothesis is that population phenotypic plasticity changes across this gradient according to ENSO intensity.

To corroborate this hypothesis, seven *Prosopis pallida* populations of North Peru following a temperature and precipitation gradient from the coast to the foothills were selected. Seeds from each population were collected to be used for a greenhouse experiment where seedlings were grown at two levels of water availability to simulate dry and extreme rainfall years. Our main objective was to understand the importance of phenotypic plasticity of *Prosopis pallida* populations as a response to high rainfall-simulated ENSO events. The specific objectives of this study were: (1) to know how key structural and physiological functional traits respond to water availability and how this response changes among populations; (2) to understand how phenotypic plasticity differs among populations; and (3) to assess whether phenotypic plasticity of functional traits in *P. pallida* populations is related to climatic factors.

Materials and methods

Study area

Six *Prosopis pallida* (Humb. & Bonpl. ex Willd.) Kunth (algarrobo) populations, located between 4º5′ – 6º22′ S and 79º00′ – 81º7′ W in the Piura Province (North-Western Peru, South America; Fig. 1), were identified. Due to one of them (Ñapique) presented high site variability related to the close proximity to a lake, this location was considered as two different populations (Ñapique Wet and Ñapique Dry being the former the closest to the lake). Therefore, we considered a total of seven populations. In all cases, forests are dominated by *P. pallida* as the main species, and were selected according an increasing climatic gradient from east to west between 15 to 153 m a.s.l., and represent the most relevant dryland forests of North Peru in terms of forest cover. Climate is characterized by hot summer and moderated wet winters

with moderate-mild annual temperature of 20.3 to 24.1 ºC. Annual precipitation averages between 7 (15 m a.s.l.) and 316 mm (232 m a.s.l.) (Table 1), occurring mainly in summer (January to March), During non-ENSO periods, there is a long-winter drought (8-9 months, from April to December), giving the study area a dry tropical climate (Bravo et al., 2003). Mean annual temperature and precipitation data for the 1950-2000 period for each population was obtained from the CRU - Global Climate data (http://www.cru.uea.ac.uk/). A standardized precipitation-evapotranspiration index (SPEI) for the same period was obtained from the climate research (CRU - http://spei.csic.es/) database (Beguería et al., 2014). Negative values of SPEI indicates drought periods and positive values indicates wetter periods. Since ENSO intensity change between locations, we also used the standard deviations of temperature, precipitation and SPEI along the 1950-2000 period at annual resolution to study the effect of climate variability on phenotypic plasticity.

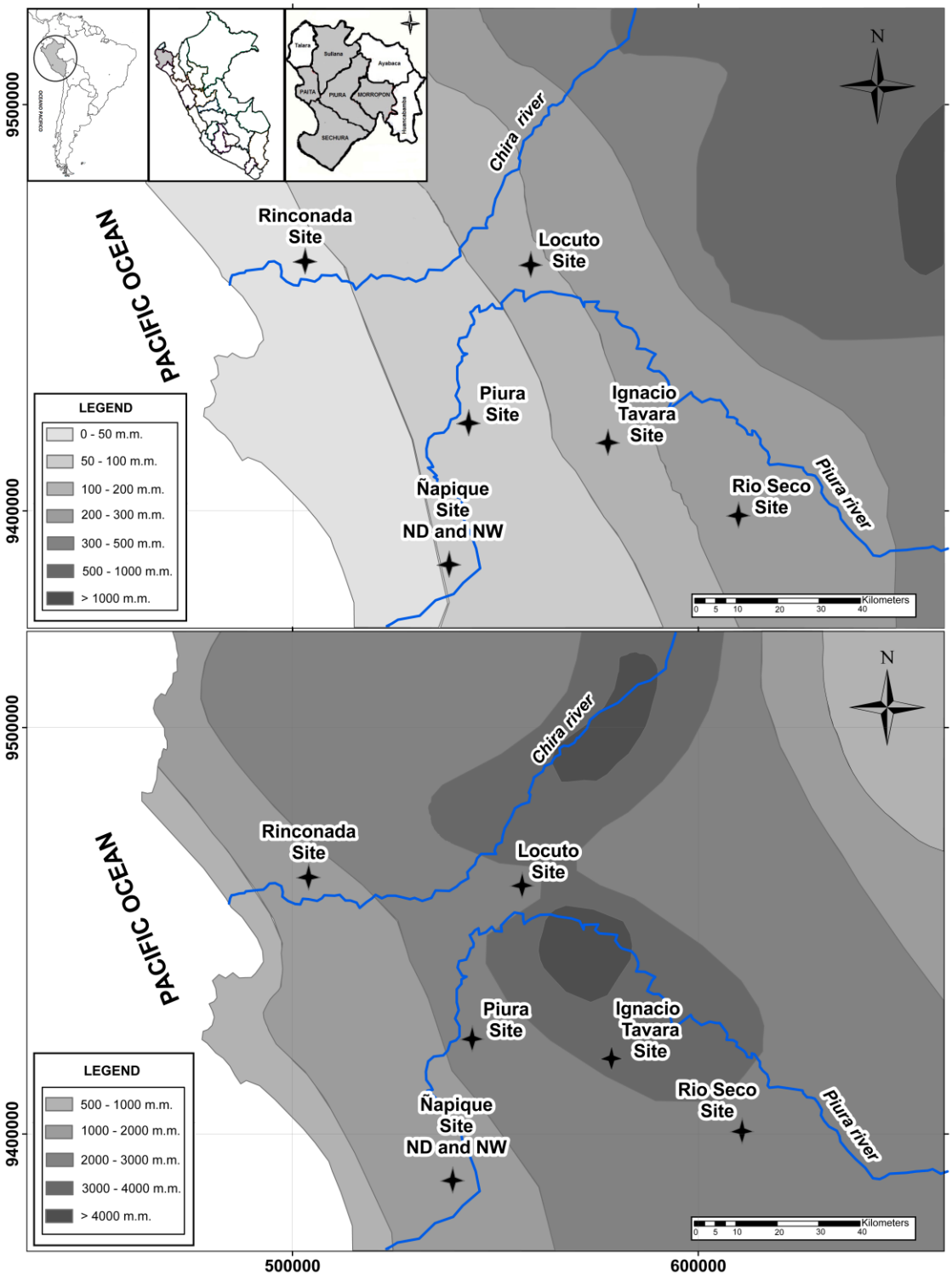

Figure 1. Localization of the seven *Prosopis pallida* populations included in this study. Average rainfall during no-ENSO years (left) and annual rainfall during the 1998 ENSO event (right) across this gradient is shown (adapted from Erdmann et al., 2008).

Seed collection and experimental design

In January 2015, pods of *Prosopis pallida* were collected at the seven populations (Fig. 1, Table 1). At each population, pods were collected from 15 different adult trees with similar features. Seeds were extracted manually using scissors and pliers, and stored in dark containers in dry conditions. To ensure germination, seeds were treated by emerging them in chloride acid 95% during 10 seconds.

Table 1. Climate description (data period: 1950-2000) and location (UTM) of *Prosopis pallida* populations included on this study. Mean annual temperature (MAT) and Mean annual precipitation (MAP) and standard deviation were obtained from CRU - Global Climate data (http://www.cru.uea.ac.uk/), while the standardized precipitation-evapotranspiration index (SPEI) was obtained from the Climate Research Unit (CRU) database (CRU - http://spei.csic.es/). Populations are ordered according to mean annual precipitation.

Zone name	Zone Code	MAP (mm)	MAT (ºC)	SPEI	Altitude (m a.s.l.)	Longitude 17 M	Latitude
Ñapique Dry	ND	7.65 ± 8	22.95 ± 0.71	-0.08 ± 0.79	15	560606	9405427
Ñapique Wet	NW	7.65 ± 8	22.95 ± 0.71	-0.08 ± 0.79	15	560606	9405427
Rinconada	RI	18.48 ± 24	22.44 ± 0.73	-0.14 ± 0.78	77	513373	9457293
Piura	PI	40.87 ± 41	23.56 ± 0.7	-0.17 ± 0.68	40	532471	9433785
Ignacio Tavara	IT	178.48 ± 123	24.11 ± 0.65	-0.22 ± 0.48	153	596277	9434052
Locuto	LO	276.94 ± 199	23.58 ± 0.64	-0.2 ± 0.53	69	584564	9422283
Rio Seco	RS	316.11 ± 148	20.32 ± 0.64	-0.17 ± 0.42	232	621417	9414217

A factorial block design with two factors (water availability and population) and 8 blocks (replicates) was carried out using PVC pots of 50 cm height and 10 cm diameter. All pots were filled with 5.5 kg of sieved soil from a natural dry forest nearby (95.6% of sand, 2.5% of lime and 1.9% of clay, pH 6.7 and field water capacity of 22 %). Nutrient concentration of the soil can be found at Table S1 (Supporting Information). To improve nutrient availability in the soil, 15 g of a slow release fertilizer (SQM-Vitas) were mixed with the soil before filling each pot. Nutrient concentration of the fertilizer can be found at Table S2 (Supporting Information). Water availability had two levels: low water availability (LW) with soil at 40% of the field capacity, and high water availability (HW) with soil at 80% of the field capacity. Five seeds were sowed in each pot, and all treatments (water availability × population) were replicated eight times (14 treatments × 8 plants, n = 112 seedlings). Five days after sowing, all seedlings in every pot were cut except the tallest. Every day,

all pots in one block were weighted to calculated daily evapotranspiration; then, all pots were watered to maintain water availability at 40 and 80% of the field capacity according to the water treatment assigned. The mean and standard error (SE) of temperature and relative humidity along the experiment were 29.15 ± 0.11°C and 62.7 ± 0.23%, respectively. Mean values of photosynthetic photon flux density (PPFD) was 623 ± 304, µmol photons m^{-2} s^{-1} measured at 12 pm solar time during different days.

Trait measurements

All plants were harvested after two months, and a week before harvest, one mature leaf per plant were taken to measure leaf mass per area (LMA; g m^{-2}) as the ratio of leaf dry mass and area. To do so, leaf surface (including petiole) was scanned and leaf area calculated using Image-Pro plus 4.5.0.29 software (Media Cybernetics, MD, USA). Leaf dry mass was measured using an analytic balance after drying the leaf for 24 hours at 60 °C. Another sample of full matured leaf was taken to measure leaf water potential using a Scholander chamber (Model 1505D PMS Instrument Company, USA) at 12 pm solar time. Leaves were then dried at 70 °C for 24 hours and stored to calculate total leaf dry mass.

Simultaneously, photosynthesis (µmol CO_2 m^{-2} s^{-1}), transpiration (E; mmol H_2O m^{-2} s^{-1}), and stomatal conductance (g_s; mmol H_2O m^{-2} s^{-1}) were measured using an infrared gas analyzer (model CI-340, CID-Bioscience Inc, USA). The net photosynthetic rate per leaf area was converted to net photosynthetic rate per unit mass ($A_{mass;}$ nmol g^{-1} s^{-1}) using the individual leaf mass per area (g m^{-2}). The measurements were made between 9:30 to 13:00 hours (local time) on cloudless days to keep photosynthetic active radiation around 600 µmol m^{-2} s^{-1} (due to the greenhouse ceiling and anti-aphid net). Instantaneous water use efficiency (WUEi, µmol CO_2/ mmol H_2O) was calculated as the ratio of net photosynthetic rate and the stomatal conductance (Quero et al., 2006).

Once all plants were harvested, plant height was measured using a metric tape, and plant biomass was divided into leaves, stems, and roots, dried a 60 ºC for 48 hours and weighed. As the substrate was very sandy, roots were

carefully cleaned by hand and the remaining soil from each pot was sieved (1 mm) to separate root hairs which were included in total root dry mass. Total plant biomass was calculated as the sum of all parts (including leaf mass from the traits measured before). Leaf (LMR), stem (SMR) and root mass ratio (RMR) were expressed in percentage by dividing each fraction by the total plant biomass and multiplied the result by 100. We also calculated the ratio between total leaf area (TLA) and the dry root mass (TLA/Root; $cm^2\ g^{-1}$) representing the ratio of water consumption and water acquisition tissues (Lopez-Iglesias et al., 2014). Total leaf area was calculated as [1/LMA] × leaf dry mass. We took a 3 cm length stem (cut below the first pair of leaves) to calculate wood density (WD), and it was totally immersed in water for 5 s in a volumetric flask to calculate the volume by the displacement method. Then the stem was dried at 70 °C for two days and WD was calculated as the ratio of dry mass and stem volume.

Evapotranspiration (ET) in each pot was calculated as the amount of water loss through the experiment as: ET = Initial mass of pot - Final mass of pot + sum of water added along the whole growth period. The plant water use efficiency was calculated as the total plant dry biomass divided by ET (Condon et al., 2002).

To study phenotypic plasticity to water availability, a relative distance plasticity index (RDPI) ranging from 0 (no plasticity) to 1 (maximal plasticity) was calculated for each trait and for each population using the following formula (Valladares et al., 2006) :

$$RDPI = \sum \frac{\left[\frac{(d_{ij} \rightarrow i'j')}{x_{ij} + x'_{i}j'}\right]}{n}$$

Where the absolute distance between two replicates (*dij* → *i'j'*) of the same population under different water treatments is divided by the sum (*xij* + *xi'j'*), considering *x* as any possible data taken, *i* as any given factor in the population treatment and *j* as the seedling number (replicate). RDPI is calculated as the sum of the relative distances obtained from all possible pairs of replicates divided by the total number of relative distances (n).

Statistical analysis

All the variables followed the assumptions of normality and homogeneity of variance, except LMA and TLA/Root that were $\log_{10}$ transformed, and ET and total plant biomass that were square root transformed. A factorial analysis of variance was performed to detect differences in population and water treatment for all variables. To study the relationship among traits, Pearson correlation analysis between all traits was made splitting the data according to the water treatment.

Also, two Principal Component Analyses (PCA) were made at low and high water availability. A correlation between the first axes of each PCA was made to determinate if the traits provide the same amount of variation between each water treatment, and if populations respond in different ways. To compare phenotypic plasticity between populations a one-way ANOVA was performed, and when the studied variables showed significant differences, a Tukey's test was used. Because RDPI ranges from 0 to 1, all data was logit transformed (x/[1-x]) prior to analysis. The proportion of the explained variance was calculated as the sum of squares of each factor divided by the total sum of squares.

To know if phenotypic plasticity was affected by climatic factors, we correlated RDPI values per trait to the mean annual precipitation (MAP), mean annual temperature (MAT) and the standardized precipitation-evapotranspiration index (SPEI) of each population. To know how the climatic variability through the ENSO affected phenotypic plasticity, we calculated the standard deviation of these climatic variables for each population and correlated them with the trait phenotypic plasticity. All the statistical analyses were carried on using STATISTICA v8.0 (StatSoft, Inc. 2007).

Results

Effect of water availability on biomass allocation and functional traits

Statistical differences were found between populations for most of the traits (Table 2, Table S3 – Supporting Information). Increase in water

availability induced changes in plant height and biomass, biomass allocation and water related traits on *P. pallida*. Moreover, for some traits (growth, evaportranspiration, water use efficiency and wood density) each population responds differently to water availability (the interaction term between the water availability and population factors was significant) (Table 2, Fig. 2). For example, plant biomass and water consumption differed between populations, and they react in different ways to the water treatment (Fig. 2a). ND population was the most notorious because of its lack of response to the water treatment in plant biomass (Fig. 2a, Table S3 – Supporting Information). NW, the nearest population to ND, also showed low differences in plant biomass between water treatments in comparison to the rest of the populations (Fig. 2a). LO and IT populations, located in more rainy locations, showed the highest values for these traits (plant biomass and water consumption) under low and high water availability (Fig. 2a, b).

Table 2. Two-way ANOVA for all morphological and physiological traits of *Prosopis pallida* considering as factors population and water treatments. The proportion of the explained variance [(SS_x/SS_{total}) × 100) and the level of significance (**P*<0.05; ***P*<0.01; ****P*<0.001) for each factor and the interactions are indicated. R^2 (× 100) is the percentage of total variance absorbed by the model. A_{mass}: Net photosynthetic rate per leaf dry mass, ET: Evapotranspiration, g_s: Transpiration rate, LMA: Leaf mass per area, LMR: Leaf mass ratio, PB: Plant biomass, PH: Plant height, RMR: Root mass ratio, SMR: Stem mass ratio, TLA/Root: Total leaf area/Root biomass, WD: Wood density, WP: Water potential, WUE, Water use efficiency and WUEi: instantaneous water use efficiency (A/g_s).

	Traits	**Population (P)**	**Water (W)**	**P x W**	**R^2x100**
Growth traits	PH	6.4***	69.9 (+)***	6.8***	81
	PB	15.0***	55.7 (+)***	9.7***	80
Biomass allocation traits	LMR	6	0.02	10.2	16
	SMR	11.1*	29.0 (+)***	6.2	46
	RMR	7	13.1 (-)***	7.8	28
	TLA/Root	5.1	7.8 (+)*	9.7	23
Water related traits	ET	7.75***	74.7 (+)***	5.7***	88
	WP	1.9	20.8 (+)***	2	25
	WUE	20.2***	35.2 (+)***	11.8***	67
Plant traits	LMA	25.0***	1.6	1.7	28
	WD	17.6*	0.4	13.8*	31
Gas exchange traits	A_{mass}	12.9*	0.8	4.3	7
	g_s	13.1*	1.9	1.1	4
	WUE_i	5.8	21.3 (-)***	3.7	31

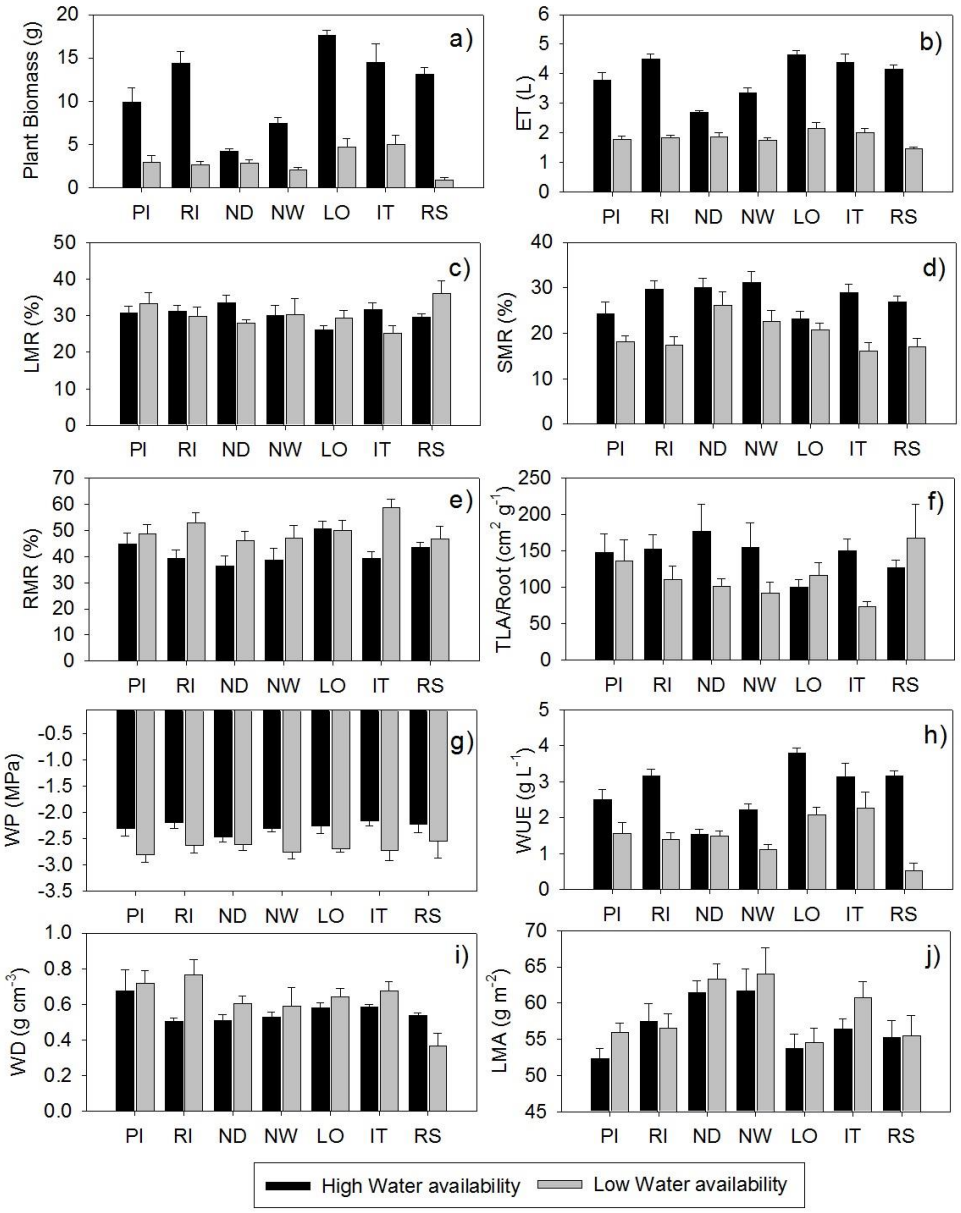

Figure 2. Morphological and physiological traits of *Prosopis pallida* populations as response to high (dark bars) and low (grey bars) water availability. ET: Evapotranspiration, LMR: Leaf mass ratio, SMR: Stem mass ratio, RMR: Root mass ratio, TLA/Root: Total leaf area/root biomass, WP: Water potential, WUE: Water use efficiency, WD: Wood density and, LMA: Leaf mass per area. Mean ± standard error.

Biomass allocation to roots and stems was significantly different between water treatments, as well as in TLA/Root proportion (Table 2). In general, plants showed a significant increase in root mass ratio (Fig. 2e) and a decrease in stem mass ratio (Fig. 2d) under the low water treatment. Differences among populations for biomass allocation were only found in the case of SMR, with ND and NW population showing a higher SMR investment than the others (Fig. 2d).

The response of water-related traits to water availability was similar than plant biomass (Table 2), with higher evapotranspiration, water potential and water use efficiency under high water treatment. Populations also differed in these traits in the response to water treatment. ND and NW populations had not a significant response for these traits to water treatment, while LO and IT populations had the highest evapotranspiration under low and high water availability (Fig. 2b, Table S2 – Supporting Information). Additionally, LMA and stem wood density did not show any significant differences between water treatments, but showed significant differences among populations (Fig. 2i and j, Table 2), suggesting a genetic control among populations on these traits. Similarly, the net photosynthetic rate per leaf dry mass and stomatal conductance did not differ between water treatments but they were significantly different among populations (Table 2). ND and NW had the highest gas exchange values, while the others populations showed similar values.

In most cases, trait relationships were the same under low and high water availability (Table S4 – Supporting Information). Total plant biomass and evapotranspiration had a positive correlation at both water treatments (Fig. 3a). Similarly, total plant biomass and RMR showed a positive correlation; however, the slope of the regression was higher under high water treatment (Fig. 3b). Other trait correlations were only found significant in one of the water treatments. For example, LMA and plant biomass were negatively correlated ($r = -0.37$; $P<0.05$) at high water availability, but showed no correlation ($r = -0.07$; $P = 0.74$) at low water availability (Fig. 3c). Also, water potential and wood density were negatively correlated under low water availability and showed no correlation under high water availability (Fig. 3d).

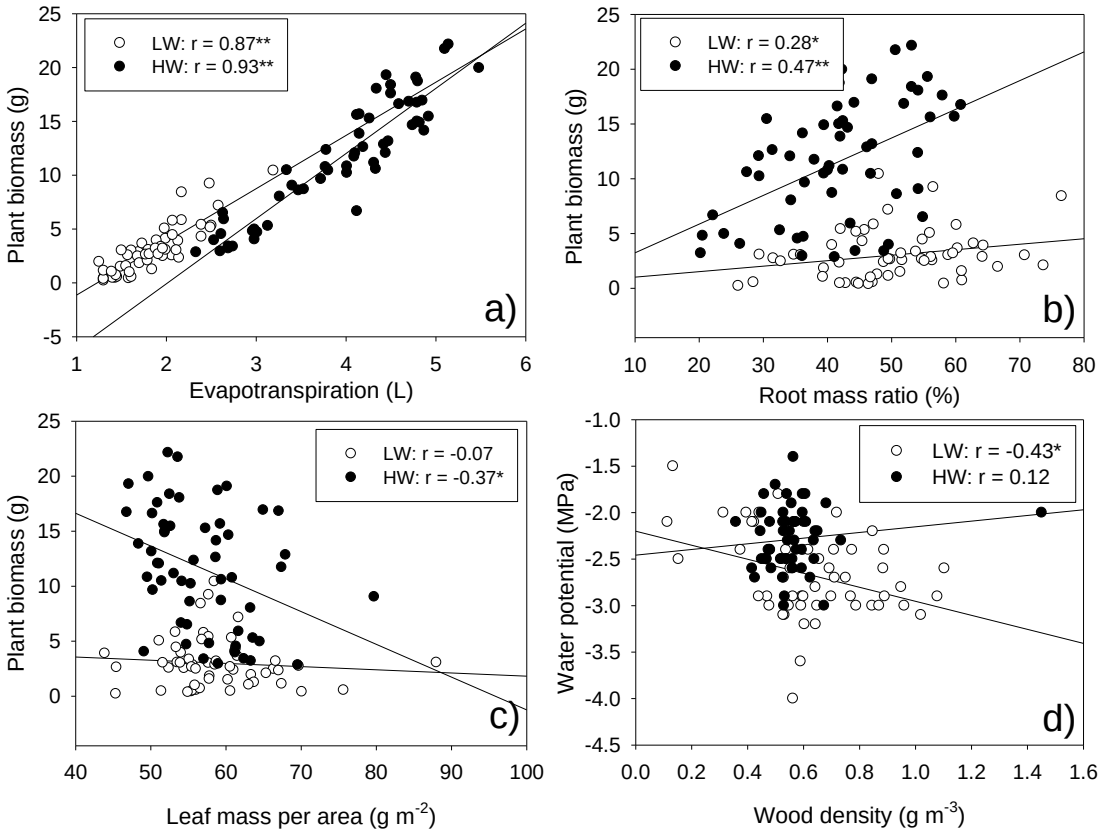

Figure 3. Relationships between plant biomass of *Prosopis pallida* with (**a**) evapotranspiration, (**b**) root mass ratio and (**c**) leaf mass per area. Relationship between leaf water potential and wood density (**d**). Black and white dots indicate high (HW) and low (LW) water availability, respectively. Correlation coefficient (r) and significance are shown. **P*<0.05; ***P*<0.01.

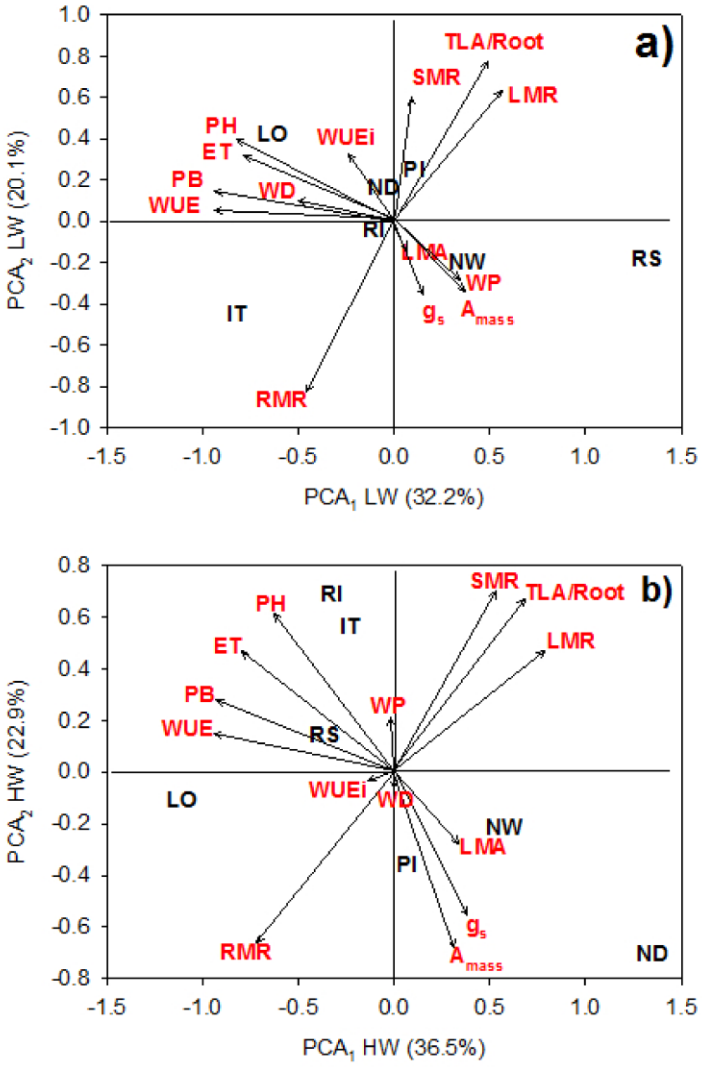

Figure 4. Principal component analysis (PCA) of morphological and physiological traits of *Prosopis pallida* under a) low (LW) and b) high (HW) water availability. Mean population score is shown in each case, see codes in Table 1. A_{mass}: Net photosynthetic rate per leaf dry mass, ET: Evapotranspiration, g_s: Transpiration rate, LMA: Leaf mass per area, LMR: Leaf mass ratio, PB: Plant biomass, PH: Plant height, RMR: Root mass ratio, SMR: Stem mass ratio, TLA/Root: Total leaf area/Root biomass, WD: Wood density, WP: Water potential, WUE, Water use efficiency and WUEi: instantaneous water use efficiency (A/g_s).

The PCA at low water availability indicates that the percentage of variation absorbed for the first two axis was 52%, similar to what has been found at high water availability (Figs. 4a and b). The traits explaining the two first PCA axes were roughly the same under low and high water availability (Table S5 – Supporting Information). Under the low water treatment, the

positive side of the first PCA axis was controlled by the TLA/Root ratio and the LMR, while the negative side was controlled by total plant biomass, and instantaneous water use efficiency. The second axis was controlled by the TLA/Root ratio and the LMR on the positive side, and RMR and stomatal conductance on the negative side. Under the high water treatment, the first axis was controlled by the same traits that under low water treatment in the positive and negative side. However, in the second axis SMR was more important than LMR in the positive side, and A_{mass} was more important than g_s in the negative side. Mean score per populations showed differences between populations and treatments. A high mean score in RS, IT and LO indicates that these populations drive the most variation of the axis 1 under low water availability, whereas ND, RS, and LO drive most variation under high water availability (Fig. 4a and b).

Variability of phenotypic plasticity to water availability among populations

Phenotypic plasticity to water availability was significantly different among populations in all variables except LMR, LMA, and WUEi (Table 3). Plant biomass, evapotranspiration, and water use efficiency showed the highest RDPI values (0.58, 0.36 and 0.33, respectively). RS was the most plastic population for these traits (0.89, 0.48, and 0.74, respectively) while ND showed the lowest RDPI values (0.24, 0.18 and 0.13, respectively). Moreover, plant biomass allocation traits, as root mass ratio, showed different plasticity values among populations (Table 3), following a different trend that plant biomass and other traits.

Plasticity of LMA showed no statistical differences between populations despite their differences in mean population traits (Table 2 and 3). This indicates that populations may have different mean values but the same response to the water treatment (Fig. 2 j).

Table 3. Mean values of plasticity index (RDPI) to water availability between populations for all traits (see Table 1 for populations code and Table 2 for variables). Subscript letters indicate Tukey post hoc results when analysis of variance was significant ($P < 0.05$).

Variables	**PI**	**RI**	**ND**	**NW**	**LO**	**IT**	**RS**	**Mean RDPI per trait**
PH	0.36^{cd}	0.47^{b}	0.20^{e}	0.43^{bc}	0.34^{d}	0.39^{cd}	0.36^{a}	0.36
PB	0.54^{c}	0.69^{b}	0.24^{d}	0.57^{bc}	0.59^{bc}	0.53^{c}	0.89^{a}	0.58
LMR	0.11	0.11	0.11	0.17	0.12	0.14	0.13	0.13
SMR	0.17^{bc}	0.27^{a}	0.16^{bc}	0.21^{ab}	0.13^{c}	0.29^{a}	0.24^{ab}	0.21
RMR	0.14^{bcd}	0.18^{ab}	0.18^{abcd}	0.18^{abc}	0.10^{cd}	0.20^{a}	0.11^{d}	0.15
TLA/Root	0.22^{b}	0.27^{ab}	0.26^{ab}	0.31^{ab}	0.21^{b}	0.33^{a}	0.23^{b}	0.26
ET	0.36^{bc}	0.42^{ab}	0.18^{d}	0.31^{c}	0.37^{bc}	0.36^{c}	0.48^{ab}	0.36
WP	0.12^{ab}	0.11^{bc}	0.07^{c}	0.11^{ab}	0.11^{bc}	0.14^{ab}	0.16^{a}	0.12
WUE	0.34^{bc}	0.40^{c}	0.13^{a}	0.14^{a}	0.30^{bc}	0.30^{b}	0.74^{d}	0.33
LMA	0.05	0.06	0.05	0.07	0.06	0.05	0.06	0.06
WD	0.19^{b}	0.30^{b}	0.13^{ab}	0.19^{ab}	0.10^{a}	0.09^{a}	0.25^{ab}	0.18
A_{mass}	0.32^{b}	0.32^{b}	0.26^{ab}	0.19^{a}	0.19^{a}	0.27^{ab}	0.32^{ab}	0.27
g_s	0.25^{bc}	0.22^{abc}	0.21^{abc}	0.15^{a}	0.15^{ab}	0.27^{bc}	0.25^{c}	0.21
WUE_i	0.11	0.13	0.16	0.15	0.09	0.12	0.11	0.12
Mean RDPI per population	0.23	0.28	0.17	0.23	0.20	0.25	0.31	

We found a positive relationship between the scores of the traits in the PCA_1 at low and high water availability, indicating that relationships among traits do not change under different water availability (Fig. 5). However, mean score per population did not show a significant correlation, suggesting that population response to water availability does not follow the same trend of trait relationships. Population phenotypic plasticity was almost significantly correlated ($r = -0.75$, $P = 0.052$) to population score of the PCA_1 under high water availability, which suggests that the differences in population response to high water are controlled by phenotypic plasticity.

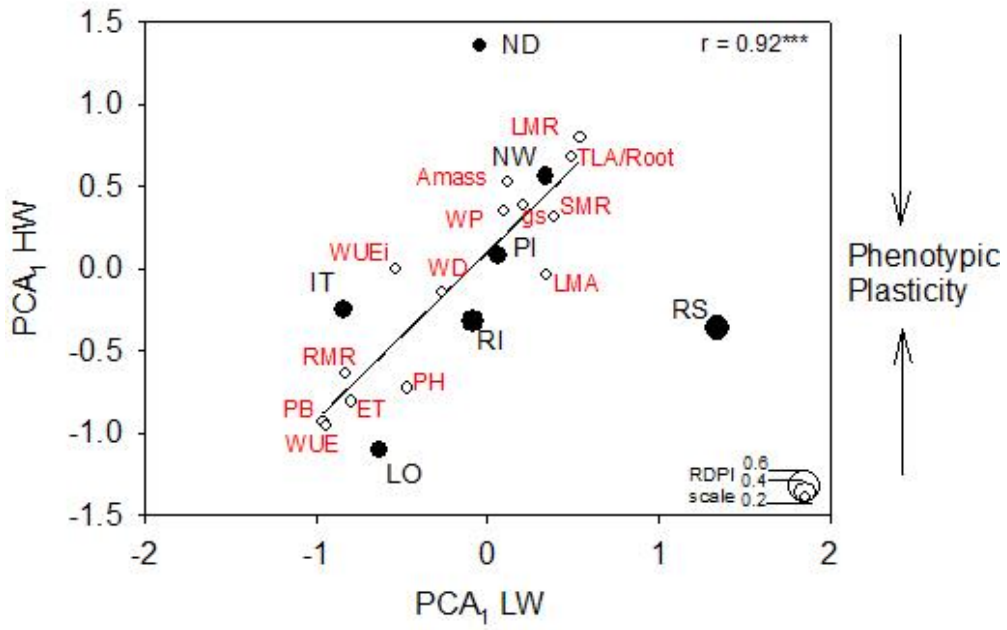

Figure 5. Relationships between the first axis of the Principal Component Analysis (PCA) of morphological and physiological traits of *Prosopis pallida* under high (HW) and low (LW) water availability (PCA_1 HW versus PCA_1 LW). Correlation coefficient and statistical significance are shown. Black dots represent score values of each population, dots size are proportional to their mean RDPI. See Table 1 for population codes and Table 2 for plant trait codes.

Functional trait plasticity in response to climatic factors

In general, phenotypic plasticity to water availability was not correlated to the climatic factors from the place of origin (Table 4). Regardless, phenotypic plasticity of plant height and WUE was negatively correlated to mean annual temperature. Moreover, WUEi was negatively correlated with MAT and its standard deviation (Fig. 6a), and positively correlated with, SPEI and its standard deviation (Fig. 6b). Also, WUEi was positively correlated with MAT standard deviation (Table 4).

Table 4. Pearson correlation coefficients between mean annual temperature (MAT), mean annual precipitation (MAP), standardized precipitation-evapotranspiration index (SPEI), and their standard deviation (SD) during the 1950-2000 period, and phenotypic plasticity of morphological and physiological traits (RDPI) of *Prosopis pallida*. Significant values ($P < 0.05$) were shown in bold font. See Table 2 for variable names.

RDPI	MAT (C°)	MAT_{SD}	MAP (mm)	MAP_{SD}	SPEI	$SPEI_{SD}$
PH	**-0.79**	-0.34	0.51	0.31	-0.22	-0.51
PB	-0.65	-0.40	0.57	0.45	-0.39	-0.54
LMR	0.00	-0.07	0.01	-0.03	0.20	-0.02
SMR	-0.21	0.06	0.00	-0.09	-0.19	-0.20
RMR	0.39	0.57	-0.65	-0.63	0.35	0.48
TLA/Root	0.33	0.28	-0.38	-0.37	0.17	0.20
ET	-0.49	-0.45	0.60	0.53	-0.59	-0.61
WP	-0.41	-0.64	0.67	0.55	-0.64	**-0.81**
WUE	**-0.76**	-0.51	0.67	0.50	-0.45	-0.68
LMA	-0.58	0.13	0.06	-0.05	0.39	0.14
WD	-0.67	0.43	-0.20	-0.35	0.29	0.25
A_{mass}	-0.20	0.30	-0.24	-0.32	-0.12	0.05
g_s	-0.37	-0.23	0.24	0.09	-0.37	-0.48
WUE_i	0.23	**0.81**	**-0.84**	**-0.84**	**0.83**	**0.85**

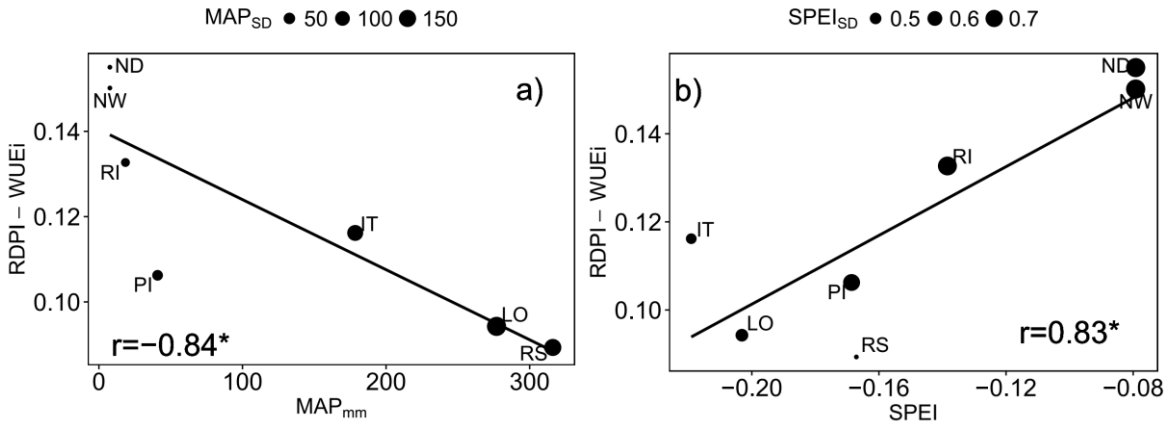

Figure 6. Relationships between trait phenotypic plasticity and mean climatic factors and its standard deviation. Relationships between phenotypic plasticity of instantaneous water use efficiency (WUEi) and mean annual precipitation (MAP) (**a**) and the standardized precipitation-evapotranspiration index SPEI (**b**) for *Prosopis pallida* populations. See Table 1 for population codes.

Discussion

Prosopis pallida is a species well known for its capacity to grow under harsh conditions and limited access to water (Khanzada et al., 1998). In Northen Peru, algarrobo populations are adapted to face extreme floods during the 1-2 year time-frame ENSO phenomenon, that appears approximately every 5 years (Tapley and Waylen, 1990). Our results showed that *P. pallida* populations response significantly to an increase in water availability, and this response is different among populations. Differences in phenotypic plasticity among traits and populations did not explain differences in plant biomass or biomass allocation. Regardless, there was not a significant relationship between plasticity and climate factors except for wood density, water potential and evapotranspiration. Thus, our hypothesis that plasticity to water availability in this arid tropical ecosystem is controlled by the climatic gradient and ENSO events has not been corroborated.

Effect of water availability on biomass allocation and functional traits

As we expected, statistical differences were found between populations for most of the traits. Differences in plant growth to water availability between populations were related to differences in water consumption. Under each water treatment, morphological and physiological changes were required to increase plant biomass. In low water availability, root mass ratio was positively correlated to plant biomass. Similar results were found in a drought experiment with *Prosopis chilensis* (López Lauenstein et al., 2012), and it is a mechanism to reduce water loss through aboveground tissues and increase water uptake underground (Liu and Stützel, 2004; Quero et al., 2006; Valladares and Sánchez-Gómez, 2006). Interestingly, we also found that root mass ratio was positively correlated to plant growth under high water availability. This could be the result of an opportunistic strategy to increase water uptake under high precipitation events, as some dendrochronological results has showed (Rodríguez et al., 2005). Thus, a significant investment in root development should come as an advantage for *P. pallida* under low and high water availability.

Aboveground tissues were also related to plant biomass. Thus, under high water availability, LMA was negatively correlated to plant biomass. This trait is commonly related with carbon uptake, growth and plant functioning in general (Niinemets, 2001). This result line up with the leaf worldwide economic spectrum (Wright et al., 2004) and previous results found in *P. pallida* (Salazar et al. Capítulo 4) which suggest that plants with low LMA leaves have higher photosynthetic rates which is related to an increase in plant growth. Even though, this trait is commonly related to drought resistance (Niinemets, 2001), we did not found a correlation between LMA and plant growth under low water availability. Similarly, Vilela *et al.* (2003) found a correlation between LMA and plant biomass in *Prosopis alba* only under high water availability, and not under drought conditions. This suggests that LMA is not involved in *P. pallida* response to water limitations, and explains why LMA did not change between water treatments.

Water consumption was also related to morphological and physiological changes in stem anatomy and functioning. Leaf water potential was lower under low water availability, a common response to drought (Quero *et al.* 2011, Bongers *et al.* 2017). A negative correlation between leaf water potential and wood density was found under low water availability. Considering that wood density is controlled by the vessels size (Alameda and Villar, 2012), this result suggest that smaller vessels are required to maintain a lower leaf water potential (López Lauenstein et al., 2012; Pockman and Sperry, 2000). Drought-tolerant plants, which showed high wood density, can stand more negative xylem pressure without cavitation (Hacke et al., 2001). Similarly, this has been found in *Prosopis flexuosa* and *P. velutina* (Lauenstein et al., 2012; Pockman and Sperry, 2000), and it show how vessel size is controlled to avoid cavitation and improve water transport under drought (Christman et al., 2012; Lovisolo et al., 1998). Similar to LMA, wood density was not affected by the water treatment, but it showed significant differences among populations. This suggests that population potential to respond to water availability is genetically controlled in these traits.

Net photosynthetic rate was not affected by water treatment, but it was significantly different among populations. These differences were mostly

noticeable in ND and NW, which have the highest A_{mass} of all populations. We found this result hard to explain, one possibility is that biochemical modifications in the leaf (as a high nitrogen concentration) may allow these populations to increase carbon uptake. According to this, a negative correlation between plant biomass and A_{mass} was found, both at high and low water availability. This correlation lacks of causation, and even though ND and NW had higher photosynthetic rate, they also had less leaf biomass, and thus less total carbon uptake than other populations. Similarly, Quero *et al.* (2008) did not find any correlation between A_{mass} and growth, although on that study carbon uptake per plant (using the A_{mass} and the leaf biomass) was positively related to growth. The same calculation of carbon uptake in our results indicate carbon uptake per plant was positively correlated to plant biomass ($r = 0.8$; $P < 0.05$), therefore photosynthetic rate per se is not as important as leaf biomass to reach a high plant biomass.

Moreover, in both PCAs (under low and high water availability) we found that plant biomass and biomass allocation were located at the extremes of both axes. Thus, these traits are equally important to establish an integrated response to water availability. Similar results were found in *Pappostipa speciosa* when the plasticity of root biomass ratio and shoot/root biomass explained its tolerance to drought (Couso and Fernández, 2012). Regardless, a shift in traits scores were found in the axis 2 of both PCA. Under low water availability, LMR and g_s showed a high score in the positive and negative side of the PCA2 respectively. While under high water availability, SMR and A_{mass} showed a high score in the positive and negative side instead. This suggests that *P. pallida* shift plant biomass allocation to increase xylem growth and carbon uptake under high water availability. Similarly, *Prosopis alpataco* and *P. argentina* also showed a high SMR under high water availability (Villagra and Cavagnaro, 2006). Thus, this unveils the physiological changes responsible for the thick tree-rings in *P. pallida* during ENSO years (López et al., 2006), and how it shift from a highly regulated system towards an exponential growth system.

Variability of phenotypic plasticity to water availability among populations

Phenotypic plasticity allows us to compare traits and populations responses to understand plant strategy to water availability. Phenotypic plasticity to water availability was significantly different among populations in all variables except LMR, LMA and WUEi. However, depending on the variable, these differences can be the result of physical limitations rather than their physiological response on water availability. Thus, absolute traits (plant height or biomass) are more plastic than plant biomass allocation traits (RMR, SMR and LMR). Phenotypic plasticity can be restricted by morphologic and ontogenetic limitations that constraint the potential plant plasticity (Valladares et al., 2007). Thus, even though RMR plasticity was relatively low, it does reflect its importance in water uptake and growth.

Moreover, population scores at each PCA showed strong differences and not follow a common pattern. Therefore, plant traits has a unique response to water availability, however, each population modify these traits differently. Differences in population response to water availability seem to be related to their phenotypic plasticity. According to Valladares (2007), trait plasticity can be restricted by trait to trait co-variation. For instance, photosynthetic rate is limited by the amount of leaf nitrogen or Rubisco activity (Quero et al., 2006; Wright et al., 2004). In our results, population with the highest scores in the PCA1 axis were the less plastic populations, while those with lowest scores were the most plastic populations (r=-0.75; P=0.052). Hence, it seems that population plasticity to water availability is higher when trait to trait co-variation is lower. This was only true for the high water availability treatment, which suggests phenotypic plasticity was related to plant response towards high precipitation events. This agrees with our previous results, where root mass ratio and LMA also showed significant correlations with plant biomass only under high water availability. It also agrees with the climatic profile of this region, dominated by dry conditions, while extreme precipitations are odd events. Thus, population plasticity provides an adaptive advantage towards high water availability.

Functional trait plasticity in response to climatic factors

Initially, we expected climatic factors significantly induce *P. pallida* phenotypic variation among populations due to their differences in water availability and temperature. Therefore, *P. pallida* optimal plasticity could be proportional to the predictability of environmental fluctuation in each location (Pohlman et al., 2005). The plasticity of plant height and water use efficiency showed a negative correlation with MAT from the place of origin. These results seems to support the idea that high plastic traits can be found under non-stress conditions because the lack of environmental pressures allow phenotypic diversity, while harsh climatic conditions will decrease traits plasticity (Bongers et al., 2017; Lande, 2009).

Likewise, variable environments could also promote higher phenotypic plasticity to enhance species persistence (Pohlman et al., 2005; Schneider and Meyer, 2017). In this regard, we found the plasticity of WUEi to be correlated positively to SPEI from the place of origin and to its standard deviation. Thus, showing that gas exchange plasticity is higher in locations with high SPEI (moister locations), and it is also higher in locations with higher fluctuations of SPEI. Therefore, phenotypic plasticity change according to the spatial and temporal variation of SPEI, a similar result was found in *Acacia spp.* were different populations showed a phenotypic plasticity adapted the background environment (Lande, 2009). The temporal variation of MAT was also positively correlated to WUEi, supporting the idea that highly variable environments promote higher phenotypic plasticity (Schneider and Meyer, 2017).

However, WUEi also showed a negative relationship with MAP and its standard deviation. Thus, neglecting the idea that phenotypic plasticity to water availability is favored under highly variable precipitation or that high phenotypic plasticity is common under non-stress climatic conditions. This result could suggest that drier locations are more sensitive to the water treatment, and thus showed a higher phenotypic plasticity. However, this does not line up with population RDPI calculated in Table 4.

Utterly, we should assume that the plastic response to water availability is the result of several external factors besides MAT, MAP and SPEI (i.e. radiation, vapor pressure deficit, among others), and probably no linear relationship can explain *P. pallida* phenotypic plasticity. Moreover, no other plant traits showed significant correlations with climatic factors. Therefore, even though plasticity of WUEi, plant height and WUE in *P. pallida* populations seems to be limited by the climatic factors, most of the variability on phenotypic plasticity among populations is not limited by the climatic conditions of this region. Thus, further research should be made to understand the genetic changes involved in phenotypic plasticity variation, probably testing the boundaries of the phenotypic expression of the highest and lowest plastic populations and their genetic pool (Schneider and Meyer, 2017).

Conclusions

We found that an increase in water availability significantly affects *P. pallida*. Under high water availability, plant biomass was positively correlated to evapotranspiration and root mass allocation, and negatively correlated to LMA. Under low water availability, WD was negatively correlated to water potential. Additionally, an increase in water availability boost the role of SMR and A_{mass} in plant trait relationships. Therefore our results prove that biomass allocation, carbon uptake, and leaf structure played shift plant phyisiology under extreme rainfall events like the ENSO.

Overall, climatic factors were not limiting or promoting phenotypic plasticity variation among populations. Some traits as WUEi, plant height and WUE showed significant relationships with SPEI, mean temperature and annual precipitation, which highlights the importance of water transport regulation under different water availability conditions.

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Supplementary Information

Table S1. Mean values ± (standard error) for soil nutrient variables. n = 15

Soil variable	Mean ± (SE)
C (mg kg^{-1})	11.4±2.5
N (mg kg^{-1})	1.2±0.2
P (mg kg^{-1})	23.3±2.8
K (mg kg^{-1})	449.3±39.2
Ca (mg kg^{-1})	3202.3±294.3
Mg (mg kg^{-1})	176.2±19.3
Fe (mg kg^{-1})	4.4±0.5
Mn (mg kg^{-1})	8.7±1.0
Cu (mg kg^{-1})	0.5±0.04
Zn (mg kg^{-1})	2.45±0.42

Table S2. Mean values for nutrient composition of the slow release fertilizer (SQM-Vitas).

Nutrient	w/w (%)	Dose per pot (g)
Total Nitrogen	14	2.1
Nitric Nitrogen	6.3	0.945
Ammoniacal Nitrogen	7.7	1.155
Phosphorous dioxide	9	1.35
Potasium oxide	15	2.25
Magnesium oxide	2	0.3
Soluble sulfur	4	0.6
Boron	0.03	0.0045
Cupper	0.02	0.003
Iron	0.4	0.06
Manganese	0.1	0.015
Molybdenum	0.02	0.003
Zinc	0.05	0.0075

Table S3. Mean trait value and standard error of different variables per population under low (LW) and high (HW) water availability. A_{mass}: Net photosynthetic rate per leaf dry mass, ET: Evapotranspiration, gs: Transpiration rate, LMA: Leaf mass per area, LMR: Leaf mass ratio, PB: Plant biomass, PH: Plant height, RMR: Root mass ratio, SMR: Stem mass ratio, TLA/Root: Total leaf area/Root biomass, WD: Wood density, WP: Water potential, WUE, Water use efficiency and WUEi: instantaneous water use efficiency (A/gs). n = 8

Variables		PI	RI	ND	NW	LO	IT	RS
PB (g)	LW	2.96±0.7	2.6±0.4	2.84±0.4	2±0.3	4.7±0.9	4.96±1.1	0.82±0.3
	HW	9.91±1.6	14.4±1.4	4.17±0.36	7.45±0.7	17.6±0.6	14.5±2.1	13.1±0.7
LMR (%)	LW	33.2±3.1	29.7±2.5	27.9±1	30.2±4.4	29.2±2.3	25.2±2.1	36.13±3.4
	HW	30.8±1.8	31.1±1.6	33.55±2.14	30.2±2.5	26.1±1.2	31.7±1.8	29.5±1.1
SMR (%)	LW	18.1±1.3	17.3±1.9	26.±3	22.5±2.5	20.6±1.7	16.1±1.9	16.96±1.9
	HW	24.2±2.7	29.6±2	30.06±1.96	31.1±2.4	23.1±1.7	28.9±1.9	26.9±1.2
RMR (%)	LW	48.6±3.6	53±3.9	46±3.6	47.3±4.7	50.1±3.8	58.7±3.2	46.91±4.6
	HW	45±4.2	39.3±3.3	36.38±3.83	38.7±4.5	50.8±2.7	39.4±2.6	43.5±1.9
TLA/Root (cm^2 g^{-1})	LW	136.4±28.9	109.9±19.3	101.3±9.8	92.1±14.6	116.7±16.7	72.8±7.1	167.3±46.1
	HW	147.3±25.9	151.8±20.5	177.1±36.5	154.2±33.8	99.7±10.5	145±16.3	126.7±10.3
WUE (g plant biomass L H_2O^{-1})	LW	1.56±0.3	1.39±0.2	1.49±0.1	1.11±0.1	2.08±0.2	2.27±0.4	0.53±0.2
	HW	2.50±0.29	3.16±0.2	1.55±0.12	2.22±0.2	3.8±0.1	3.1±0.4	3.16±0.1
WP (MPa)	LW	-2.8±-0.1	-2.6±0.1	-2.6±0.1	-2.8±0.1	-2.7±0.1	-2.7±0.2	-2.5±0.3
	HW	-2.3±0.1	-2.2±0.1	-2.5±0.1	-2.3±0.1	-2.3±0.1	-2.2±0.1	-2.2±0.2
ET (L)	LW	1.77±0.1	1.83±0.1	1.88±0.1	1.74±0.1	2.15±0.2	2.02±0.1	1.45±0.1
	HW	3.78±0.25	4.49±0.2	2.68±0.08	3.36±0.2	4.64±0.15	4.39±0.3	4.15±0.2
WD (g cm^{-3})	LW	0.72±0.1	0.77±0.1	0.60±0.04	0.59±0.1	0.64±0.04	0.68±0.05	0.37±0.1
	HW	0.68±0.11	0.51±0.02	0.51±0.03	0.53±0.02	0.58±0.03	0.58±0.01	0.54±0.01
LMA (g m^{-2})	LW	55.9±1.3	56.5±1.9	63.3±2.2	64±3.6	54.5±1.9	60.8±2.2	55.51±2.8
	HW	52.35±1.37	57.4±2.5	61.50±1.51	61.7±3	53.7±2	56.4±1.4	55.3±2.3
PH (cm)	LW	27.2±3.9	28±3	33.8±2.7	25.8±2.4	37.6±3.7	33.1±4.9	12.9±2.1
	HW	55.5±4.1	76.3±3	50.6±2.3	64.7±4.1	74.3±2.5	71.7±5.6	69.3±2.5
A_{mass} (nmol CO_2 g^{-1} s^{-1})	LW	125.4±31.4	131.9±13.2	145.5±20.2	166.3±19	133.2±17.3	97.5±20.3	151.9±24.2

Variables		PI	RI	ND	NW	LO	IT	RS
E (mmol H_20 $m^{-2}s^{-1}$)	HW	130.3±19.9	90.5±21.5	177.3±24.4	147.5±18.3	112.7±11.8	102.7±9.9	115.9±19.3
	LW	1.6±0.2	1.5±0.2	2.1±0.3	1.8±0.2	1.5±0.1	1.8±0.4	1.7±0.2
gs (mmo lH_20 $m^{-2}s^{-1}$)	HW	2.1±0.3	2.0±0.3	2.1±0.2	1.8±0.1	1.9±0.2	1.8±0.3	1.9±0.4
	LW	61.9±14.2	56.6±6.1	78.4±10.6	76.9±9	53.5±4.3	61.5±10.7	63±10.1
WUEi (umol CO_2 mmol H_2O^{-1})	HW	71.3±8.9	63.3±11.5	97.2±12.4	81.6±7.8	65.9±5.7	62±7.5	64.3±11.9
	LW	0.14±0.01	0.16±0.01	0.14±0.01	0.14±0.01	0.15	0.14±0.01	0.13±0.01
	HW	0.13±0.01	0.12±0.01	0.11±0.01	0.11±0.01	0.13±0.01	0.13±0.01	0.13±0.01

Table S4. Pearson correlation coefficients between morphological and physiological traits of *Prosopis pallida* Correlation between plants under high water availability is shown in the upper right table. Correlation between plants under low water availability is shown in the down left table. * P <0.05, ** P < 0.01. Abbreviations as in Table 2. (n = 56 for each treatment).

	PH	PB	LMR	SMR	RMR	TLA/ Root	ET	WP	WUE	LMA	WD	A_{mass}	E	g_s	WUE_i
PH		0.79**	-0.31*	0.27*	-0.01	-0.06	0.84**	0.13	0.71**	-0.25	-0.12	-0.45*	-0.18	-0.39*	-0.01
PB	0.91**		-0.57**	-0.29*	0.47**	-0.43*	0.93**	0.08	0.97**	-0.37*	-0.04	-0.42*	-0.17	-0.39*	0.10
LMR	-0.22	-0.38*		0.59**	-0.87**	0.92**	-0.38*	0.11	-0.65**	0.08	0.02	-0.09	0.14	0.03	-0.04
SMR	0.31*	-0.01	0.14		-0.91**	0.76**	-0.09	0.08	-0.41*	0.11	-0.12	-0.22	0.08	-0.05	-0.14
RMR	-0.02	0.28*	-0.82**	-0.69**		-0.93**	0.25	-0.11	0.58**	-0.11	0.06	0.18	-0.12	0.01	0.11
TLA/ Root	-0.09	-0.34*	0.80**	0.41*	-0.82**		-0.21	0.14	-0.53**	-0.17	-0.02	-0.16	0.15	-0.06	-0.05
ET	0.87**	0.87**	-0.17	0.13	0.05	-0.13		0.15	0.83**	-0.38*	-0.04	-0.48**	-0.15	-0.42*	0.05
WP	-0.22	-0.23	0.04	-0.09	0.02	0.03	-0.11		0.03	-0.17	0.12	0.07	-0.06	-0.05	0.11
WUE	0.83**	0.97**	-0.42*	-0.08	0.36*	-0.39*	0.75**	-0.25		-0.35*	-0.04	-0.36*	-0.16	-0.35*	0.12
LMA	-0.01	-0.07	0.00	0.25	-0.14	-0.35*	-0.03	0.08	-0.10		-0.06	0.05	-0.07	0.25	-0.24
WD	0.46*	0.46*	-0.13	-0.01	0.10	-0.17	0.4	-0.43*	0.43*	-0.03		-0.03	0.25	-0.05	0.13
A_{mass}	-0.24	-0.33*	-0.01	0.03	-0.01	0.02	-0.23	0.36*	-0.35*	-0.02	0.03		0.19	0.73**	0.08
E	0.05	-0.03	-0.08	0.16	-0.03	-0.02	0.06	0.13	-0.06	0.15	-0.09	0.34*		0.51**	0.20
g_s	-0.04	-0.08	-0.09	0.10	0.01	-0.18	-0.03	0.23	-0.08	0.29*	0.11	0.72**	0.69**		-0.14
WUE_i	0.21	0.16	-0.06	0.04	0.02	0.15	0.19	-0.21	0.10	-0.26	0.15	-0.19	-0.10	-0.41*	

Table S5. Variable scores for the principal component analysis at high and low water availability treatment. See Table S2 for variable names.

	Low Water Treatment		**High Water Treatment**	
	Factor 1	Factor 2	Factor 1	Factor 2
PH	**-0.83**	0.40	-0.64	0.62
PB	**-0.96**	0.14	**-0.94**	0.28
LMR	0.55	0.64	**0.79**	0.47
SMR	0.10	0.60	0.53	0.70
RMR	-0.46	**-0.82**	-0.73	**-0.67**
TLA/Root	0.50	**0.78**	0.68	**0.67**
ET	**-0.80**	0.32	**-0.81**	0.47
WP	0.34	-0.29	-0.02	0.21
WUE	-0.24	0.32	-0.14	-0.03
LMA	0.07	-0.14	0.34	-0.28
WD	-0.52	0.11	0.00	-0.07
A_{mass}	0.37	-0.34	0.31	**-0.68**
g_s	0.14	-0.37	0.38	-0.56
WUEi	**-0.94**	0.05	**-0.95**	0.14

Capítulo 4

Intraspecific leaf functional trait variability of eight *Prosopis pallida* tree populations along a climatic gradient of the dry forests of northern Peru

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Abstract

We studied intraspecific trait variability (ITV) in functional leaf traits of *Prosopis pallida* trees located in eight populations along a climatic gradient on the Peruvian coast. The objectives were (1) to determine the relative importance of ITV at different ecological scales; (2) to understand how functional leaf traits relate to each other, and (3) to know the main climatic factors related to ITV in *P. pallida*. We used the restricted maximum likelihood method to decompose the variance across three nested ecological scales (population, plot, and tree level). The relative variance decomposition showed that tree level was the main source of variation for leaf chemical composition and stomatal size and density, whereas the plot and population levels were the main sources of variation for gas exchange and structural variables, respectively. Leaf ITV followed the general trends of the *leaf economic spectrum*, with negative relationships of leaf mass per area with both photosynthetic rate and leaf nitrogen. Precipitation was not related to any of the leaf traits, while mean annual temperature was correlated negatively with leaf relative water content and positively with water use efficiency. Our results highlight the importance of ITV in *P. pallida* and the possible impact of climate change.

Keywords: algarrobo; intraspecific variability; leaf mass per area; net photosynthetic rate; mean annual temperature; water use efficiency

Introduction

The study of functional trait variation is useful to describe and understand plant physiology and community composition (de la Riva et al., 2015; Hulshof and Swenson, 2010; Volf et al., 2016). The causes of this variation could be interspecific and/or intraspecific, the latter being considered less important. However, recent studies indicate that intraspecific trait variability (ITV) can provide meaningful information about trait responses along environmental gradients (Laforest-Lapointe et al., 2014; Siefert et al., 2015), agricultural crop performance (Gagliardi et al., 2015; Okubo et al., 2012), and genetic selection (Arntz and Delph, 2001). ITV may explain how certain species can pass through both biotic and abiotic filters to maintain viable populations, promoting species coexistence (de la Riva et al., 2015; Jung et al., 2010; Messier et al., 2010).

ITV can be studied according to different levels of ecological scales: trees, plots, and populations, (Albert et al., 2010; Messier et al., 2010), which may provide different explanations of the causes of functional trait variability. At the population level, plant trait variation is affected by climatic factors such as temperature and precipitation (Fajardo and Piper, 2011; Richardson et al., 2013). In this sense, Albert et al. (2010) found that 60% of the maximum height variation of *Dryas octopetala* L. was explained at the population level, and this variable had strong relationships with temperature and light radiation. Thus, high ITV at the population level may indicate that it arises from differences in climatic factors. However, other factors - such as soil texture, successional stage, and disturbance regimes - should not be ignored. The plot level, a subsample unit inside the population level, may also show trait variations and can provide information about the response to small-scale abiotic factors such as water and nutrient availability, soil compaction, and salinity. Plot-level variation may indicate factors limiting plant recruitment, the successional stage, and the ecological strategy of a species (Messier et al., 2010). On other hand, at the tree level, ITV may result from intra and/or interspecific site-competition for nutrients, light, or water (Albert et al., 2010; Messier et al., 2010; Schemske et al., 2009). High genetic variability within populations could also be responsible for variations at the tree level. However, genetic differences should be more relevant between populations, where gene flow may be reduced.

Studies of plant functional traits have already found that leaf structure (LMA, leaf dry mass per area) and leaf lifespan are negatively related to leaf physiology (A_{mass}, net photosynthetic rate per unit leaf dry mass) and leaf chemical composition (LNC, leaf nitrogen concentration) (Poorter et al., 2009; Wright et al., 2004). These trade-offs between functional leaf traits represent the *leaf economic spectrum* (Wright et al., 2004), one extreme being represented by species with an *acquisitive resource strategy* (low LMA and high A_{mass}) and the opposite extreme by species showing a *conservative resource strategy* (Wright et al., 2004). At the intraspecific level, leaf traits may change among populations, the resource use strategy shifting to best suit the current environmental conditions. In this sense, Gagliardi et al. (2015) found that functional leaf traits in *Coffea arabica* covaried in patterns consistent with the *leaf economic spectrum*.

Previous works have studied ITV using experimental designs that included a wide study area with great changes in altitude and latitude (Fajardo and Piper, 2011; Hulshof and Swenson, 2010; Richardson et al., 2013). Both of these latter variables strongly influence temperature, irradiance, and several other environmental factors - such as soil texture and soil nutrient and water availability (Valladares et al., 2007). For example, the study of Fajardo and Piper (2011) covered an extensive area, with latitude from 36º to 46º south in Chile, with great differences in altitude and annual precipitation. Similarly, the work of Richardson et al. (2013) covered an area with latitude from 41º to 47º south in New Zealand, with large changes in altitude (from 0 to 1400 m a.s.l.), temperature and precipitation. Studies with many simultaneous stresses, strong environmental gradient intensity, and high genetic variability introduce strong ecological limits to phenotypic plasticity, hindering ITV (Albert, 2015; Valladares et al., 2007). Although these studies are interesting as they explore wide environmental gradients to understand the importance of environmental factors in ITV, covariation between climatic variables means that they overlap in their effects and influence one another, making it difficult to study them independently. Thus, experimental designs that avoid the absence of strong simultaneous stresses should also be considered.

The algarrobo (*Prosopis pallida* H. et Bonpl. ex Willd. H.B.K.), a leguminous tree adapted to long periods of drought, is a key species of the dry forests of the eastern coasts of Peru and Ecuador, and it represents approximately 61% of plant cover in the dry forests (Bravo et al., 2003). Because of its relevance in rural economy, most of the previous research about algarrobo has been focused on food applications (Grados et al., 2003; Liu et al., 2011). However, studies related to physiology and ecological characteristics are limited (but see Harris et al., 2003; Padrón and Navarro-Cerrillo, 2004) or they are focused on other species of this genera, such as: *P. alba*, *P. chilensis*, *P. juliflora*, *P. fleuxosa*, or *P. nigra* (Delatorre et al., 2008; López Lauenstein et al., 2012). Thus, ecological and physiological studies of *P. pallida* are needed to understand the importance of ITV in a climate change scenario.

In our case, we study the ITV in functional leaf traits of *P. pallida* in eight populations located in the dry forests of northern Peru. These eight populations follow a decreasing precipitation gradient and an increasing

temperature gradient from east to west. These climatic factors have shown to have a significant impact on leaf traits, increasing the leaf dry mass per area and decreasing the leaf nitrogen concentration in hotter and drier conditions (Moles et al., 2014). Thus, these effects can change the relationships between these variables and other related leaf traits. In our environmental gradient, there is no significant change in altitude (15 to 232 m a.s.l.), latitude (5-6º south), or soil texture (sand fraction over 64% in all locations). Thus, no changes in atmospheric pressure, oxygen concentration, or temperature are found due to the altitudinal differences. Therefore, we expected that ITV may respond clearly and independently to variation in temperature and/or precipitation along the environmental gradient. The hypothesis underpinning this study is that it is possible to identify changes in the ITV of *P. pallida* at different spatial scales (tree, plot, and population) and that ITV at the population level could be related to the climatic variation from the coast to the foothills of the Andes in northern Peru.

We measured structural (LMA; LDMC, leaf dry matter content; stomatal size and density), physiological (A_{mass}, maximum photosynthetic rate per unit leaf dry mass; g_s, stomatal conductance; LRWC, leaf relative water content), and chemical (C and N concentrations) leaf traits. Considering the severe water limitation in dry forests, structural and functional traits related to water exchange - such as stomatal density, stomatal size, and LRWC - were also included. These variables have been related to physiological traits like transpiration and photosynthetic rate (Wu et al., 2014); structural traits like LMA (Meziane and Shipley, 2001); and survival under water limitation and salinity (Orsini et al., 2012; Sun et al., 2014).

The general objective of this study was to assess the differential response of the ITV of *P. pallida* along a climatic gradient of precipitation and temperature in the dry forest of northern Peru. The specific objectives were (1) to determine the relative importance of the source of variation of ITV at different ecological scales (population, plot, or tree level); (2) to discover if, at the intraspecific level, leaf traits relationships follow the *leaf economic spectrum* generally described for interspecific studies; (3) to understand how functional traits at the population scale are related to environmental factors such as temperature and/or precipitation. These

results will give us information about the importance of intraspecific variability and the possible impact of climate change in the dry forest.

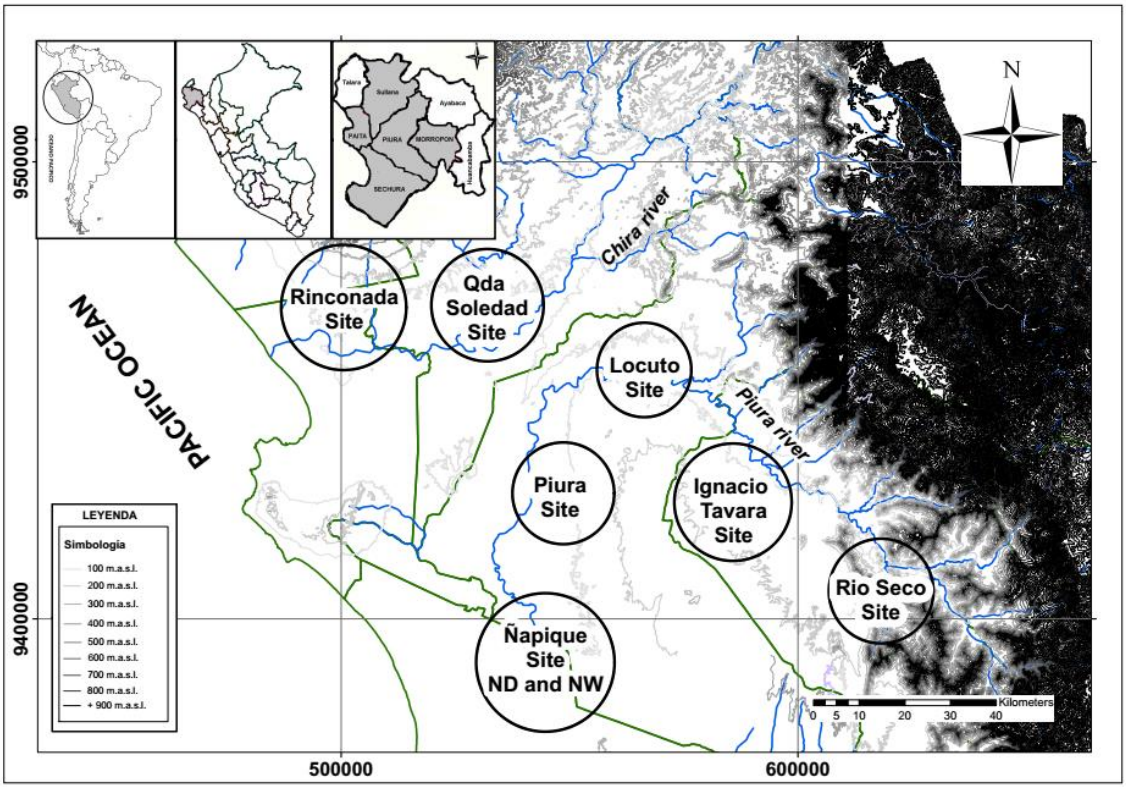

Figure 1. Localization of the eight *Prosopis pallida* populations included in this study.

Materials and methods

Study sites

The *P. pallida* dry forests studied are located at 4º5′ – 6º22′ S and 79º00′ – 81º7′ W in the Piura province of north-western Peru, South America (hereafter abbreviated as Piura) (Fig. 1). The mean annual precipitation is between 48 mm and 354 mm, with moderately mild mean annual temperatures of 23.2 to 24.8 ºC, and the altitude ranges from 15 to 232 m a.s.l (Rollenbeck et al., 2015). The dominant soils result from aeolian or alluvial deposition and the topography is characterized by semi-desert plains (INRENA 1998). The study area consists mainly of forests, in which the principal species is *P. pallida*, accompanied by *Loxopterygium huasango* Spruce ex Engl. (hualtaco), *Bursera graveolens* (Kunth) Triana and Planch. (palo santo), and *Capparis angulata* R. & P. (sapote) in the tree stratum.

Unlike most tropical regions, the climatic conditions in this area are characterized by a lack of precipitation events and high climatic stability.

Due to the thermal inertia of the Pacific Ocean, the sea surface temperature and air temperature are highly linked in this region and, because of the Humboldt current system and wind formations, are the main predictors of precipitation. Therefore, an increase in temperature is associated with higher precipitation, and a significant spatial variation exists across the region, from the coast to the foothills. A high temporal variation in weather conditions comes only from extreme precipitation events, related to a rise in temperature during the El Niño Southern Oscillation (ENSO). However, this event only appears every ~7 years, and the rest of the time this region faces highly stable climatic conditions. Rollenbeck et al. (2015) found that during no-ENSO years the temperature follows a regular annual cycle and that it can be closely fitted with a sine wave with a phase length of one year and an amplitude of 7-9 ºC.

Sampling design and data collection

Seven algarrobo populations, ranging from the coast to foothills, were selected to cover a variation in temperature and precipitation (Table 1, Fig. 1). Since one of them (Ñapique) presented high site variability related to the close proximity to a lake, we considered two different populations (Ñapique Wet and Ñapique Dry, the former being closer to the lake). Therefore, we considered a total of eight populations. Data sampling was carried out during a no-ENSO year (2014). Thus, the climatic conditions were stable. The mean annual temperature and precipitation for the 1950-2000 period for each site were obtained from the WorldClim - Global Climate data (Hijmans et al., 2005). To know if the mean environmental data obtained from WorldClim were representative of the environmental conditions of the year of sampling (2014), we used the Climate Research Unit (CRU) database (https://crudata.uea.ac.uk/cru/data/hrg/cru_ts_4.00/ge/) to obtain annual temperature and precipitation data from each location. These data were obtained from extrapolation of the few climate stations located in the region. We correlated the CRU data of 2014 (the year of sampling) and WorldClim data and proved that the two data sources were strongly correlated (Appendix Fig. A1). Thus, we are confident that the environmental data represent the climate variations during no-ENSO years.

Table 1. Climate description and location (UTM) of the studied zones in northern Peru. Data obtained from WorldClim-Global Climate (Hijmans et al., 2005) for the period 1950-2000. MAP: Mean annual precipitation, MAT: Mean annual temperature. Zones were ordered according to altitude.

Zone name	Zone Code	MAP (mm)	MAT (ºC)	Altitude (m a.s.l.)	Longitude	Latitude
Ñapique Wet	NW	81	23.7	15	17 M 533068	9388956
Ñapique Dry	ND	81	23.7	15	17 M 533068	9388956
Quebrada Soledad	QS	73	23.9	61	17 M 519339	9455070
Piura	PI	48	23.9	73	17 M 532471	9433785
Locuto	LO	157	24.3	69	17 M 568326	9453687
Rinconada	RI	52	23.4	97	17 M 498171	9457866
Ignacio Tavara	TA	208	24.8	153	17 M 577205	9433091
Rio Seco	RS	354	23.2	232	17 M 617468	9415078

To cover all the spatial and microclimatic variability, three plots of 10000 m^2 were chosen, considering similar tree density, the presence or absence of other species, and the edge effect within each site. The distance between plots ranged from 300 to 4000 m, to avoid pseudo replication. The soils in all plots and sites had a sandy texture (98% sand), except Rio Seco (RS) with a loam-sandy texture (29% silt and 7% clay). Within each plot, a random sampling inventory was developed and five adult trees of *P. pallida*, with a basal stem diameter exceeding 10 cm, were selected as experimental units for all plant measurements. Individual tree locations were recorded with a real-time differential global positioning system (GPSMAP 76CSx - Garmin USA International, Inc; Estimated Position Error <1 m).

All the leaf traits measurements were taken in summer (between January and March), which is the growing season of *P. pallida* due to the rainfall episodes and temperature conditions. For physiological measurements (see below), three mature sun-exposed leaves with no signs of damage were randomly selected in each tree. The chosen leaves were located at a tree height between 1.5 and 2.5 m to facilitate data acquisition. Net photosynthetic rate (µmol CO_2 m^{-2} s^{-1}), transpiration rate (E; mmol H_2O m^{-2} s^{-1}), and stomatal conductance (g_s; mmol H_2O m^{-2} s^{-1}) were measured using an infrared gas analyzer (CID-Bioscience Inc, model CI-340). The measurements were made between 8:00 and 13:00 h (local time) on cloudless days, to achieve a mean (± SD) photosynthetically active radiation of 1279 ± 29 µmol m^{-2} s^{-1}. The average temperature during measurements was 37.6 ± 3.7 ºC. The net photosynthetic rate per unit leaf area was converted to net photosynthetic rate per leaf dry mass ($A_{mass;}$ nmol

g^{-1} s^{-1}) using the individual leaf dry mass per area (g m^{-2}) (see methods below). The water use efficiency (WUE, nmol CO_2/ mmol H_2O) was calculated as the ratio of the net photosynthetic rate to stomatal conductance (Quero et al., 2006). Some data were discarded due to the fact that measurements were made too early in the morning when the photosynthetic radiation was very low. Therefore, in some cases the mean data of individual trees for these physiological traits were calculated using between 10 and 15 measurements.

Additionally, in each tree a fully expanded, sun exposed branch was selected and mature leaves with no signs of damage were collected in hermetic bags and transported to the laboratory to obtain the leaf area and dry mass. The leaves (including petiole) were scanned and leaf area was calculated using Image-Pro plus 4.5.0.29 software (Media Cybernetics, MD, USA). Leaf dry mass was measured, after drying the leaves for 24 h at 80 ºC, using an analytical balance. Leaf dry mass per area (LMA) was calculated as the ratio of leaf dry mass to area. A subsample of leaves from each tree was taken to analyze the carbon (LCC, %) and nitrogen (LNC, %) concentrations. For that, leaves were ground with a stainless steel mill and the C and N concentrations were measured using an elemental analyzer (Eurovector EA 3000; EuroVector SpA, Milan, Italy).

A subsample of fresh leaves was selected and taken in hermetic containers (previously weighed) to calculate the leaf relative water content (LRWC). In the laboratory, the containers were weighed and the leaves were taken to full water saturation and weighed again 10 hours later. Finally, the leaves were dried for 24 h at 80 ºC and weighed again. The LRWC was calculated using the following equation (Bussotti and Pollastrini, 2015): LRWC = (Fresh leaf mass - Dry leaf mass) × 100 / (Fully water-saturated leaf mass - Dry leaf mass). The leaf dry matter content (LDMC) was calculated using the following equation: LDMC = (Dry leaf mass / Fully water-saturated leaf mass) × 100.

To measure stomatal size and stomatal density, imprints of the leaf adaxial and abaxial surfaces were taken from a subsample of leaves using clear nail polish (Sampson, 1961). After five minutes, the imprints were taken using a transparent tape and then examined with a light microscope (Zeiss model Axioskop, Germany). Digital pictures of all imprints were taken, calibrated using a calibration slide micrometer, and analyzed using Adobe Photoshop 3CS (Adobe Systems). Stomatal density was calculated

as the number of stomata (adaxial and abaxial surfaces) per unit area. In about ten stomata per leaf, we measured the long and short axis of each stoma, to calculate a proxy of stomatal area using the ellipse equation.

Statistical analysis

Prior to statistical analysis, all data taken from the same tree were averaged to use as a statistical unit. We examined the fit of all variables to the assumptions of normality and homogeneity of variance, using the Kolmogorov–Smirnov and Levene test, respectively. When the data did not fit a normal distribution, they were normalized by $\log_{10}$ transformations. Once the basic requirements had been met, structural and physiological variables were analyzed statistically using a nested analysis of variance (ANOVA) with the aov function of R (nesting the tree inside the plot and this inside the population) (R Development Core Team 2007 version 3.2.2). When the studied variables showed significant differences at the population level, Tukey's test was used to detect differences between populations (Sokal and Rohlf, 1995). Then, we calculated the percentage of variance explained by the population, plot, and tree levels, following Messier et al. (2010). For that, we fitted a general linear model to the variance across the three scales nested one into another (i.e. nested ANOVA with random effects) in this increasing order: tree, plot, and population, using a restricted maximum likelihood (REML) method in the lme function of the "nlme" package of R.

To explore the relationships between leaf traits, Pearson's correlation analyses between physiological and structural traits at the tree level were performed. Multivariate relationships among the variables were studied using a Principal Component Analysis (PCA), to determine the variables that explained most of the variation. For the PCA, all leaf traits measured were included except E (highly correlated with g_s) and the adaxial stomatal area (highly correlated with the abaxial stomatal area). To study the effect of climatic factors on leaf traits, we used the mean data from every population and performed Pearson's correlation analyses between leaf traits and climatic factors (mean annual temperature, MAT; and mean annual precipitation, MAP). Also, correlations between the PCA axes and climatic factors were made. The Pearson's correlation analyses and PCA were performed using STATISTICA v8.0 (StatSoft, Inc. 2007).

Results

Sources of intraspecific leaf traits variability

All the leaf traits studied differed statistically among the eight populations, except for stomatal density (Table 2). Structural leaf traits (such as LMA and LDMC) had their highest values in Ignacio Tavara and Quebrada Soledad, two of the sites with higher mean annual temperature. The Ignacio Tavara population had also the lowest LRWC, A_{mass}, and g_s (Table 2). Despite the significant variability of the leaf chemistry traits among populations, LCC and LNC had the lowest coefficients of variation among all the traits (3.4 and 16.7, respectively). In the case of the two Ñapique populations, we expected to find large differences in leaf traits related to the proximity to a lake. However, in general, we did not find significant differences between these two populations, although Ñapique Wet, the population closest to the lake, had a higher mean value for LRWC and g_s and a lower LNC.

Table 2. Mean ± standard error (n= 10 - 15) of leaf traits of *Prosopis pallida* populations in in northern Peru (Piura Region). LMA: leaf dry mass per area; LDMC: leaf dry matter content; LRWC: leaf relative water content; A_{mass}: net photosynthetic rate per leaf dry mass; g_s: stomatal conductance; WUE: water use efficiency; stomatal density (number of stomata per mm^2); LNC: leaf nitrogen concentration; LCC: leaf carbon concentration. Different letters indicate significant differences between populations at $P \leq 0.05$ (One way ANOVA; Tukey test). The coefficient of variation (CV) within each population is shown. The significance of Population (Pop) and Plot are shown as NS, non-significant; **P<0.01; ***P<0.001.

Zone Code	LMA (g m^{-2})	LDMC (%)	LRWC (%)	A_{mass} (nmol CO_2 g^{-1} s^{-1})	g_s (mmol H_2O m^{-2} s^{-1})	WUE (nmol CO_2 mmol H_2O^{-1})	Stomatal density (# per mm^2)	Abaxial stomatal area (μm^2)	Adaxial stomatal area (μm^2)	LNC (%)	LCC (%)
NW	85.4±3.36^{ab}	28.0±0.84^{ab}	85.4±2.1^{a}	77.3±8^{ab}	28.8±2.8^{a}	0.245±0.03^{bc}	1229±53	84.1±10.2^{a}	85.8±8.4^{a}	3.15±0.08^{c}	44.21± 0.5^{ab}
ND	87.9±2.9^{ab}	27.8±0.64^{ab}	75.9±2.1^{b}	47.0±9.1^{bc}	15.9±1.8^{b}	0.254±0.04^{abc}	1462±152	70.1±11.2^{ab}	59.7±3.8^{ab}	3.54±0.09^{b}	45.72± 0.3^{a}
QS	97.5±3.63^{a}	33.4±0.91^{a}	56.7±1.1^{c}	75.6±10.8^{ab}	29.2±5^{a}	0.289±0.02^{ab}	1870±184	51.6±5.7^{abc}	46.1±3.7^{bc}	3.40±0.11^{bc}	43.93± 0.4^{ab}
PI	66.1±2.67^{cd}	23.5±0.9^{b}	75.6±2.2^{b}	99.4±17.4^{ab}	25.0±3.68^{ab}	0.251±0.01^{abc}	1656±163	54.7±6.3^{abc}	46.8±8.4^{bc}	3.69±0.15^{ab}	43.89±0.3^{b}
LO	65.1±3.61^{d}	25.1±1.35^{b}	74.1±2.2^{b}	107.2±9.2^{a}	29.2±2.4^{a}	0.259±0.02^{abc}	1781±268	40.4±4.0^{c}	38.6±3.5^{c}	4.21±0.13^{a}	44.14± 0.5^{ab}
RI	64.1±4.14^{d}	24.4±0.93^{b}	86.4±1.8^{a}	85.4±15.0^{ab}	23.5±2.9^{ab}	0.202±0.02^{c}	1316±121	59.2±6.2^{abc}	47.0±5.1^{bc}	3.75±0.19^{ab}	43.6± 0.2^{b}
TA	94.7±2.96^{a}	33.2±0.45^{a}	51.6±1.3^{c}	32.7±6.9^{c}	9.5±1.9^{c}	0.336±0.02^{a}	1387±128	47.9±5.0^{bc}	43.3±2.9^{bc}	3.24±0.13^{bc}	43.86± 0.4^{b}
RS	78.7±3.54^{bc}	27.9±1.76^{ab}	89.8±1.5^{a}	59.4±11.0^{abc}	23.0±4.3^{ab}	0.188±0.02^{c}	1520±128	81.1±7.2^{a}	79.2±5.5^{a}	3.69±0.16^{ab}	44.87±0.2^{ab}
CV (%)	22.5	18.5	19.9	57.8	51.4	31.7	35	43.3	40.3	16.8	3.5
Pop	***	***	***	***	***	***	NS	***	***	***	**
Plot	NS	NS	NS	***	***	**	NS	NS	NS	NS	NS

The population factor explained a high percentage of the variance (40 to 80%) of the structural leaf traits (such as LMA, LDMC, and LRWC) (Fig. 2). The plot level accounted for a significant amount of the variance in the gas exchange variables (e.g. A_{mass}, g_s, and WUE) (Fig. 2). Variables related to stomatal variation (stomatal density and stomatal size), leaf chemistry (LCC and LNC), and leaf structure (LMA and LDMC) were explained to a high degree (>50%) at the tree level (Table 2, Fig. 2).

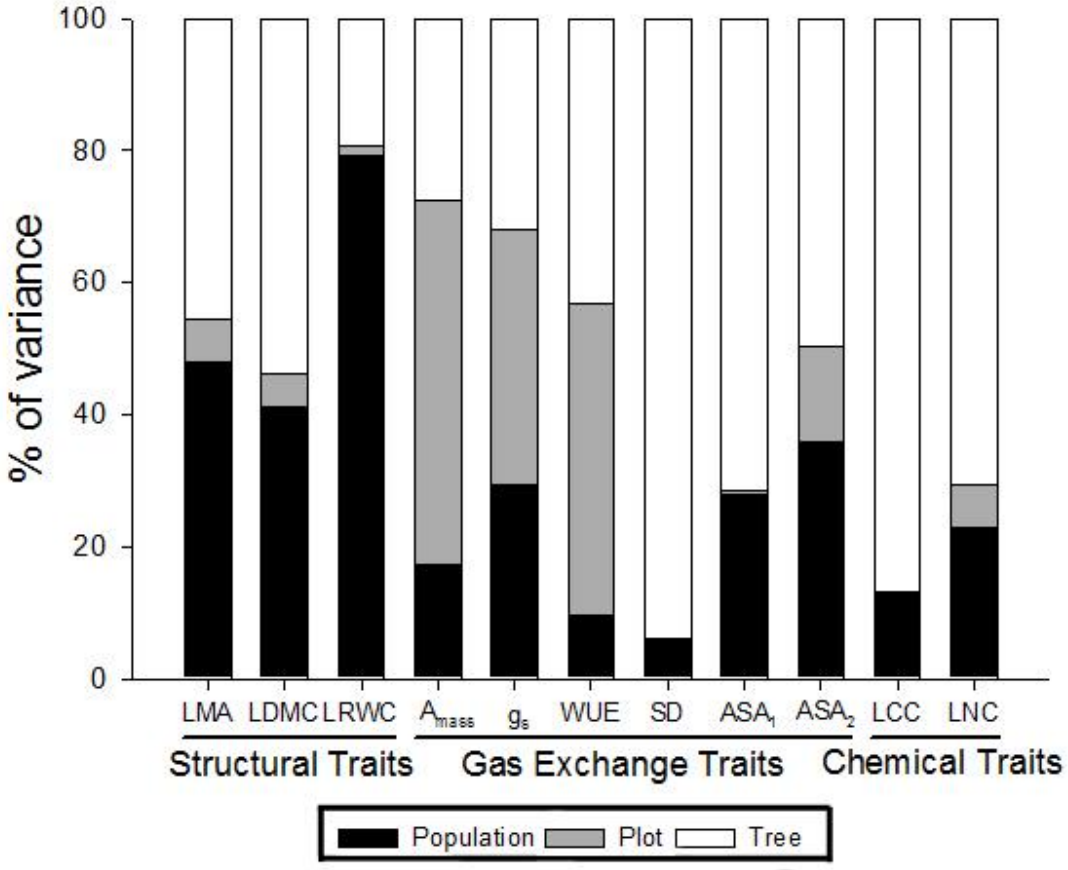

Figure 2. Source of variation within variables. Relative variance decomposition at the tree (white bar), plot (gray bar), and population (dark bar) levels for LMA: leaf dry mass per area; LDMC: leaf dry matter content; LRWC: leaf relative water content; A_{mass}: net photosynthetic rate per leaf dry mass; g_s: stomatal conductance; WUE: water use efficiency; SD: stomatal density (number of stomas per mm^2); ASA1: abaxial stomatal area; ASA2: adaxial stomatal area; LCC: leaf carbon concentration; and LNC: leaf nitrogen concentration.

Leaf traits relationships

The LMA was correlated negatively with A_{mass} and LNC (Fig. 3A, B), following the trend of the *leaf economic spectrum* (Appendix, Fig. A2), and positively with LDMC (Appendix, Table A1). The LRWC was negatively correlated with LDMC and WUE (Fig. 3C, D).

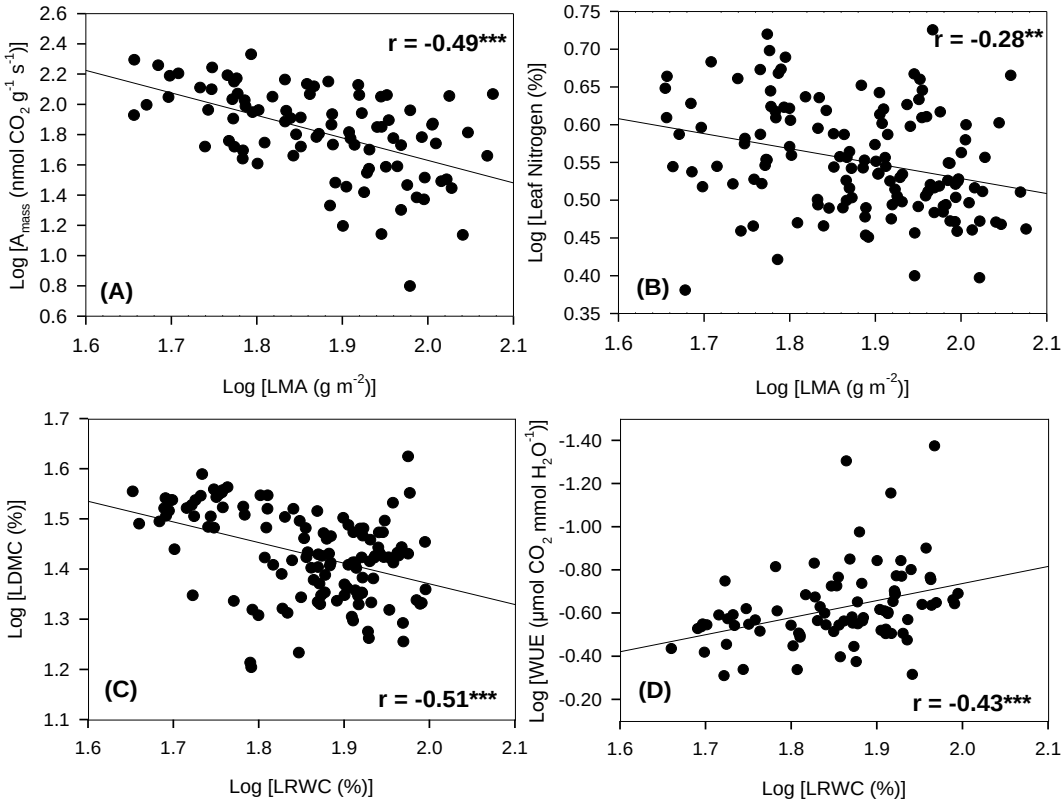

Figure 3. Bivariate trait correlations at the tree level. Relationship of leaf dry mass per area (LMA) with (**A**) net photosynthetic rate per leaf dry mass (A_{mass}) and (**B**) leaf nitrogen concentration. Relationships of leaf relative water content (LRWC) with (**C**) leaf dry matter content (LDMC), and (**D**) water use efficiency (WUE). The correlation coefficient (r) and the significance are shown. **P*<0.05; ****P*<0.001.

The PCA was used to reduce multivariate variation and determine which variables explained most of the variation in leaf traits. The first axis of the PCA (accounting for 28% of the variance) was correlated positively with LMA and LDMC and negatively with gas exchange variables (A_{mass} and g_s) (Fig. 4). This axis corresponded in the positive side with most of the trees studied in Ignacio Tavara and Quebrada Soledad, the populations with higher mean annual temperature, and in the negative side with the Locuto and Piura populations. The second axis of the PCA (explaining 17% of the variance) was mainly related to the increase in LRWC and stomatal area, and to the decrease in WUE and stomatal density (Fig. 4). As expected, the gas exchange variables (A_{mass} and g_s) were positively correlated with each other, as were the adaxial and abaxial stomatal areas (Appendix, Table A1).

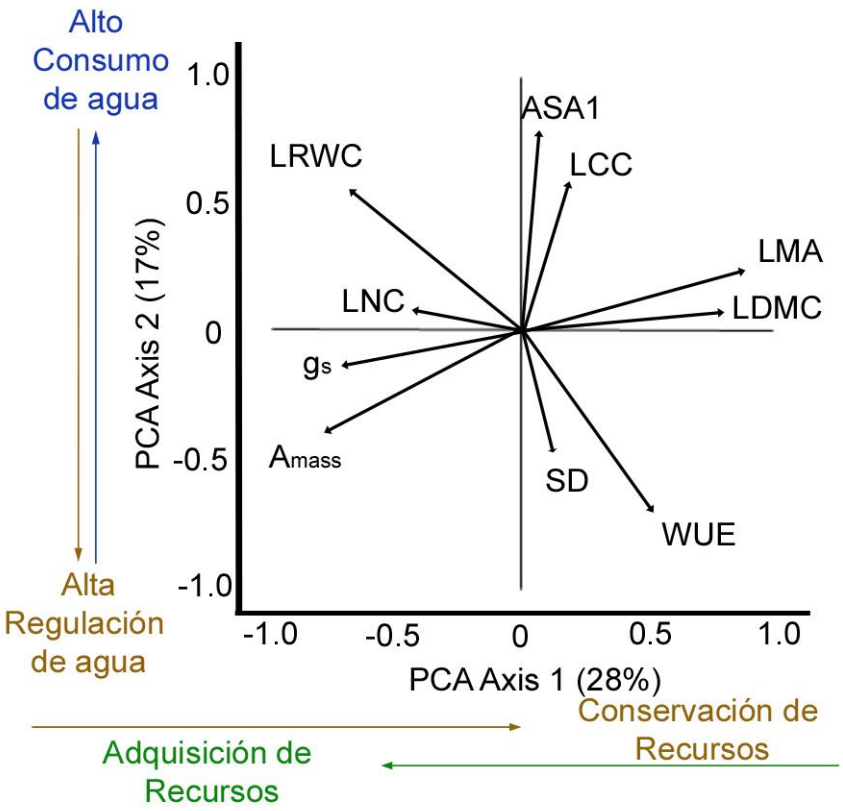

Figure 4. Principal component analysis (PCA) to determine the multivariate relationships among leaf traits: abaxial stomatal area (ASA1), leaf carbon concentration (LCC), leaf dry matter content (LDMC), leaf dry mass per area (LMA), leaf nitrogen concentration (LNC), leaf relative water content (LRWC), net photosynthetic rate per leaf dry mass (A_{mass}), stomatal conductance (g_s), stomatal density (SD), and water use efficiency (WUE).

Relationships between leaf traits and environmental factors

At the population level, the mean leaf traits did not show any relationship with mean annual precipitation (Table 3). However, mean annual temperature was correlated negatively with LRWC and abaxial stomatal area, and positively with WUE (Table 3). Thus, mean annual temperature was positively related to the main axis 2 of the PCA (Fig. 5), which is controlled by water regulation traits. Gas exchange variables were not correlated with mean annual temperature or precipitation (Table 3).

Table 3. Pearson correlation coefficients between leaf traits of *P. pallida* and mean annual temperature (MAT) and precipitation (MAP) at the population level. **P*<0.05, ***P*<0.01. For abbreviations see Table 2. Bold font means significant values.

	LMA	**LDMC**	**LRWC**	**A_{mass}**	**g_s**	**WUE**	**Stomatal Density**	**Abaxial stomatal area**	**Adaxial stomatal area**	**LCC**	**LNC**
MAT	0.28	0.41	**-0.82***	-0.17	-0.39	**0.91****	0.20	**-0.71***	-0.59	-0.32	-0.10
MAP	0.12	0.24	-0.10	-0.40	-0.27	0.16	-0.01	0.22	0.32	0.26	0.11

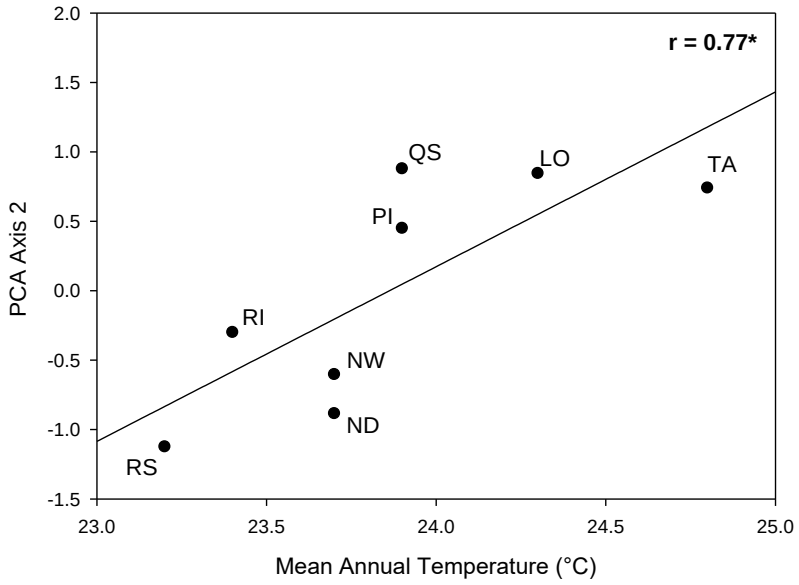

Figure 5. Relationship of mean annual temperature with Axis 2 of the PCA at the population level. **P*<0.05.

Discussion

We found high trait variability among the eight *P. pallida* populations of the dry forests along a climatic gradient in northern Peru. Structural (LMA) and gas exchange (A_{mass}) traits were highly variable in comparison to trait variation in the leaf economic spectrum; however, this was not the case for the leaf chemical composition (Appendix Fig. A2). The tree, plot, and population levels explained the variation of different leaf traits at differing extents. At the tree level, functional intraspecific leaf trait variations followed the general trends of the *leaf economic spectrum*, described, in general, at the interspecific level. At the population level, the variation in functional traits did not follow the precipitation gradient, but showed a significant relationship between water regulation variables and mean annual temperature.

Sources of intraspecific trait variability

Variations of leaf functional traits differed between distinct ecological scales. Differences in the variance explained by the population, plot, and tree levels allow us to understand which one of these scales contributes the most to the traits variation. At the population level, ITV is generally affected by both external conditions - such as climatic factors, disturbance regime, or soil fertility - and internal conditions, such as

succession stages, plant phenology, or ontogeny (Kazakou et al., 2009; Messier et al., 2010). In our case, LRWC, LMA and LDMC showed a high amount of variation explained at the population level. The latter two variables are associated strongly with plant strategies, and are mostly known to be associated with climatic factors (Moles et al., 2014; Wright et al., 2005). Arid and semiarid ecosystems tend to have high-LMA leaves, which might be an adaptation to protect leaf function under dry conditions (Niinemets, 2001).

At the plot level, ITV may be due to local processes - such as the edaphic, hydric, and topographic conditions. Results for variance partitioning commonly show a small percentage at this level (Albert et al., 2010; Messier et al., 2010); however, it depends on the plot variability. In our case, the variability of gas exchange traits (A_{mass}, g_s, and WUE) was mainly explained at the plot level (Fig. 2). Similarly, in *P. juliflora*, gas exchange traits were limited by high solar radiation, which can change according to the population, position of plot (edge effect), or degree of herbivory (Elfadl and Luukkanen, 2006).

At the tree level, ITV may be due to relatively small-scale factors like air humidity, wind, resource availability, radiation regime, and genetic variation (Messier et al., 2010). In our study, a high amount of variance was explained at the tree level for chemical composition traits (LCC and LNC), stomatal variables (stomatal density and stomatal size), and structural traits (LMA and LDMC). Differences in LNC may indicate differences in soil fertility, resource availability, or degree of root development among trees (Guevara et al., 2010; Luo et al., 2016; Siefert et al., 2015). However, considering that LNC had the lowest coefficient of variation among all the traits and that most of this variation was at the tree level, we may assume that the variation comes from intrinsic factors such as root development and not from extrinsic factors like soil fertility or water availability (Decuyper et al., 2016). Of all the leaf traits, LMA is arguably the most studied, and represents the link between leaf structure and function (Poorter et al., 2009; Siefert et al., 2015; Wright et al., 2004). Almost half of the variance in LMA was explained at the tree level, and similar results (52%) have been found for *Nothofagus* sp. in New Zealand across environmental gradients (Fajardo and Piper, 2011), for many tropical species (48%) in Panama (Messier et al., 2010), and for perennial species (70%) in Belgium (Harzé et al., 2016). For LDMC, the variance

percentage explained at the tree level was even higher (53%) than in other studies (Albert et al., 2010; Messier et al., 2010). This contrasts with recent studies indicating that leaf structure may be constrained around specific values within each species (Siefert et al., 2015). However, Harzé et al. (2016) showed that LMA and LDMC can be highly variable under different soil water conditions. While groundwater might be equally heterogeneous at the tree, plot, and population scales, we believe that root development could have differed among trees. Decuyper (2016) found differences in root growth at the tree and population levels. This suggests that limited root development has a detrimental effect in sites with less groundwater. Considering that *P. pallida* is a phreatic species with facultative deciduous leaves, it is possible that its leaf structure variability depends on the underground water supply.

Leaf traits relationships

The ITV at the tree level also provides basic information about phenotypic plasticity and how the variations in leaf traits are related to each other, to optimize plant performance. The LMA and LDMC are key leaf traits that describe leaf structure and leaf mass investment. They are highly correlated, and related to leaf lifespan, leaf chemical composition, and leaf gas exchange rate (Poorter et al., 2009; Wright et al., 2004). In our case, LMA and LDMC in one extreme and A_{mass} and g_s in the opposite extreme were the main drivers of variation in the first axis of the PCA. Similar results with A_{mass}, LNC, LMA, and LDMC have been found in coffee (Gagliardi et al., 2015) and *Nothofagus* sp. (Richardson et al., 2013), suggesting that leaf mass investment may be a decisive factor in leaf traits variations. The relationship between LMA and A_{mass} has long been studied in plant ecology (Donovan et al., 2011; Wright et al., 2004). There was no evidence of this relationship at the intraspecific level in *Prosopis* species (Vilela et al., 2003); however, ITV studies have found this type of relationship for other species (Gagliardi et al., 2015; Richardson et al., 2013). Comparing our results with the data of the *leaf economic spectrum* (Wright et al., 2004), we could consider *P. pallida* a resource acquisitive species with quick returns from leaf investments (Appendix, Fig. A2). This is supported by the high LNC, which was also negatively correlated with LMA.

The abaxial stomatal area (ASA1), LRWC, and water use efficiency

(WUE) were the main drivers of variation in the second main axis of the PCA, which showed a dichotomy between water consumption traits (ASA and LRWC) and water regulation traits (WUE and stomatal density). This is supported by the strong negative relationship of LRWC with both LDMC and WUE (Fig. 3C and 3D). In *P. juliflora*, stomatal control is quite sensitive to humidity and temperature, thereby regulating water loss and gas exchange (Elfadl and Luukkanen, 2006). This indicates that water control variables are associated with the optimization of gas exchange in *P. pallida*, which reduces water consumption and increases WUE when water availability is low.

Leaf traits response to climatic factors

Despite the high intraspecific leaf traits variability and the strong precipitation gradient across all the populations studied, there was no relationship between mean annual precipitation and any of the leaf traits studied. Similar results were found in *Prosopis alba* and *P. flexuosa*, where WUE was not affected by a decrease in water availability (Vilela et al., 2003; Villagra et al., 2005). Dryland ecosystems, and specifically dry forests in northern Peru, show a long period of drought over the year, with about seven months without rain (Appendix, Fig. A3). Moreover, this region receives extremely low annual rainfall (less than 300 mm); far lower than most *Prosopis* dryland forests (300-600 mm). Hence, its intensity and periodicity may explain why functional leaf traits variation does not relate to annual precipitation, at least during no-ENSO years.

The lack of response to precipitation suggests that *P. pallida* has some compensatory physiological mechanism that counteracts leaf water loss - such as transpiration reduction, minimum photosynthetic rates, low water potential, and underground water uptake - even at high temperature (Delatorre et al., 2008). In fact, low water potential and high underground water availability in *Prosopis tamarugo* have been used to hypothesize a water movement cycle, where water flow from deep roots to the leaf during the day, and backward flow during the night to a root mat under the soil surface, allows growth and production in dry conditions (Chávez et al., 2012; Garrido et al., 2016). This type of root morphology is common in *P. flexuosa* populations, where the water table is close to the surface (4-7 m depth) and provides a reliable way to grow and reproduce with less than 350 mm of mean annual precipitation (Guevara et al., 2010). According to

our results and site characteristics, we could expect a similar water movement mechanism in *P. pallida* - at least in populations where high humidity benefits stomatal control, gas exchange (Elfadl and Luukkanen, 2006), and water flow through the roots.

It is worth noting that the inclusion of a population located close to a lake (Ñapique Wet) did not influence the lack of relationship between precipitation and functional traits. Ñapique Wet and Ñapique Dry showed similar mean values of all traits except LRWC, g_s, and LNC. Also, excluding NW from the correlation analysis did not change the main results. This also suggests that the underground water depth is not a decisive factor in functional trait variation, at least in this location.

Among the other environmental factors studied, mean annual temperature was highly correlated to the main axis 2 of the PCA. In other studies, temperature has been the main source of variation and is also known to affect leaf mass investment variables such as LMA (Fajardo and Piper, 2011; Poorter et al., 2009), LDMC (Albert et al., 2010), and leaf thickness (Richardson et al., 2013). In *Prosopis* sp., variation in temperature has been found to affect leaf physiology and radial growth (Morales et al., 2001). Delatorre (2008) found that temperature affects *Prosopis chilensis* in the same way as water deficit, reducing transpiration and the photosynthesis rate due to stomatal closure (Elfadl and Luukkanen, 2006). However, we did not find a relationship between mean annual temperature and A_{mass}, LMA, or g_s - probably because mean annual temperature variability was lower (23.2 - 24.8 ºC) than in other studies and these traits only present significant variation under large changes of environmental factors (Messier et al., 2010). Despite that, we found a strong negative correlation of mean annual temperature with both LRWC and abaxial stomatal area; and a strong positive correlation with WUE. Moreover, these three variables, aside from leaf stomatal density, were the main drivers of variability in the second main axis of the PCA, which explains why MAT was highly correlated with it. A significant increase in WUE has been considered a mechanism to cope with drought and arid conditions, favoring leaf water conservation (Arntz and Delph, 2001). This indicates that water regulation variables may play an important role in leaf physiology in *P. pallida*, even under small variations of mean temperature (± 2 °C). A relationship between stomatal control, gas exchange, and temperature has been found also in the genus *Prosopis* (Delatorre et al.,

2008; Elfadl and Luukkanen, 2006), supporting our findings. In our case, there was a negative correlation between WUE and g_s (r=-0.28, $P<0.05$). Thus, the increase in water regulation seems to be controlled by stomatal closure and water flux through the leaf, without strongly affecting carbon flux through the leaf.

Due to the wind flow direction, Rio Seco showed the highest MAP. However, due to the weakness of the wind flow at 150 km from the coast, warm breeze from the coast mix with cold breeze from the mountain and reduce air temperature in RS. Thus, it also showed the lowest MAT in the region. This allows us to study the effect of high water availability without the stress that comes from high temperature. Our results show that while precipitation has a higher variation along the climatic gradient its effect does not have the same significance as the change in temperature. Therefore, water regulation traits seem to be restricted when temperature increases, even if precipitation increases, in this climatic gradient. However, excluding the Rio Seco population there is a significant correlation between MAT and MAP, and therefore, we can not conclude that water regulation traits respond better to temperature than to precipitation. In this sense, Rio Seco could be considered as an outlier in our dataset because it has also a soil texture less sandy that the other studied places and this could affect the relationships with water related traits. However, there are *Prosopis pallida* populations in places with environmental conditions similar to Rio Seco (Mantaro Valley and Cajamarca, near the Andes Mountains), therefore Rio Seco could not be strictly an outlier. In any case, similar populations of *Prosopis pallida* with less sandy soil and located near the Andes Mountains should be studied to reach an absolute corroboration of the differential effects of temperature and rainfall and confirm the trend between water regulation traits and MAT (Bravo et al., 2003).

However, excluding the RS population there is a significant correlation between MAT and MAP, and therefore, water regulation traits could respond to variation in both precipitation and temperature. Hence, similar populations with less sandy soil and located near the Andes Mountains should be studied to reach an absolute corroboration of the differential effects of temperature and precipitation and to confirm the trend of water regulation traits in response to MAT (Bravo et al., 2003).

Current IPCC reports estimate that precipitation will increase in the 3.4 (5°N-5°S, 170°W-120°W) and 1+2 (0°-10°S, 90°W-80°W) regions of the Pacific Ocean (including the north Peruvian coast) due to the increase in sea surface temperature (Bates et al., 2008). Our results suggest that the increase in temperature will have a highly detrimental effect on *P. pallida* populations, and the increase in precipitation might not be enough to compensate it. Moreover, theoretical considerations suggest that changes in precipitation, unlike temperature, are difficult to predict. This could explain why mean annual temperature in the area has been rising in the last decade without a significant increase in precipitation. Under these conditions, *P. pallida* populations would start to struggle, water loss through the leaf will increase stomatal closure, and, as a consequence, gas exchange will be reduced until hydraulic conductivity cannot be sustained (Bongers et al., 2017). Forest conservation will depend on the natural selection of resistance phenotypes if this trend is fully confirmed. Its high ITV at the tree level suggests that *P. pallida* has high genetic variability; however, survival of new seedlings depends heavily on ENSO events (Squeo et al., 2007). Therefore, the frequency and intensity of these extreme climatic events may determine the success and maintenance of the forest in the future.

Conclusions

Functional leaf traits of *Prosopis pallida* have shown high intraspecific variability. Relative variance decomposition shows that leaf structure is highly variable at the population level, while gas exchange variations are higher at the plot level and stomatal variation and leaf chemistry variations are higher at the tree level. The relationships between leaf traits followed the general pattern of the "*leaf economic spectrum*", with one extreme showing a fast resource acquisition strategy (high-A_{mass} and low-LMA leaves) and the other extreme a conservative resource strategy (with the opposite traits). The leaf water economy also showed a dichotomy among individuals, with high-water-consumption leaves (at one end) having bigger stomata and high LRWC, and high-water-regulation leaves having high stomatal density and WUE. Mean annual temperature seems to play a more important role in the intraspecific variability of leaf traits than mean annual precipitation. However, further research along this gradient is required to confirm this trend. These results provide an

insightful understanding of leaf trait adaptations in the dry forest and in a climate change scenario.

Acknowledgments

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Supplementary Information

Figure A1. Pearson correlation between WorldClim (1950-2000) and CRU (2014) data for mean annual temperature (a) and mean annual precipitation (b). The CRU data were obtained at https://crudata.uea.ac.uk/cru/data/hrg/cru_ts_4.00/ge/.

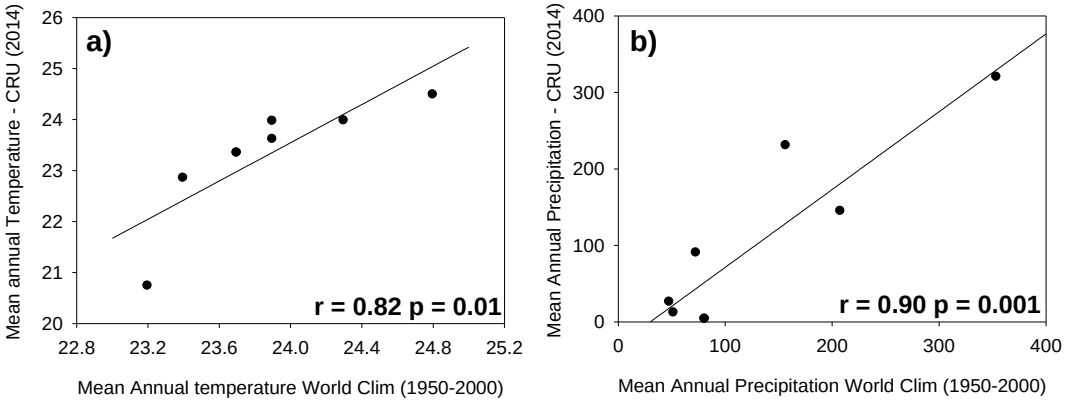


Figure A2. Multiple scatterplot between Log leaf dry mass per area (LMA) and **A)** Log net photosynthetic rate per unit leaf dry mass (A_{mass}) and **B)** Log nitrogen concentration (LNC). Dark dots represent the *leaf economic spectrum* data from Wright et al. (2004). White dots represent *Prosopis pallida* data of this study. The correlation coefficient (r) and the significance are shown. **, $P<0.01$; ***, $P<0.001$.

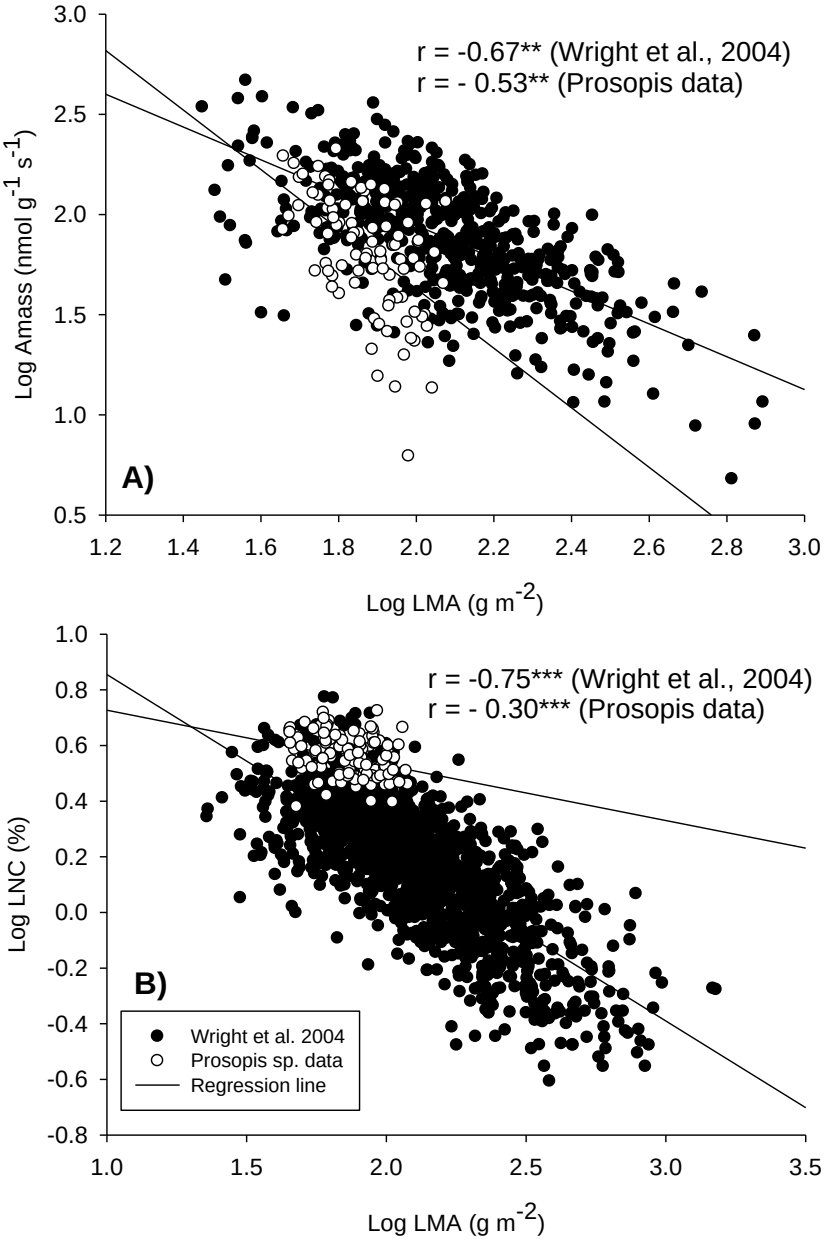
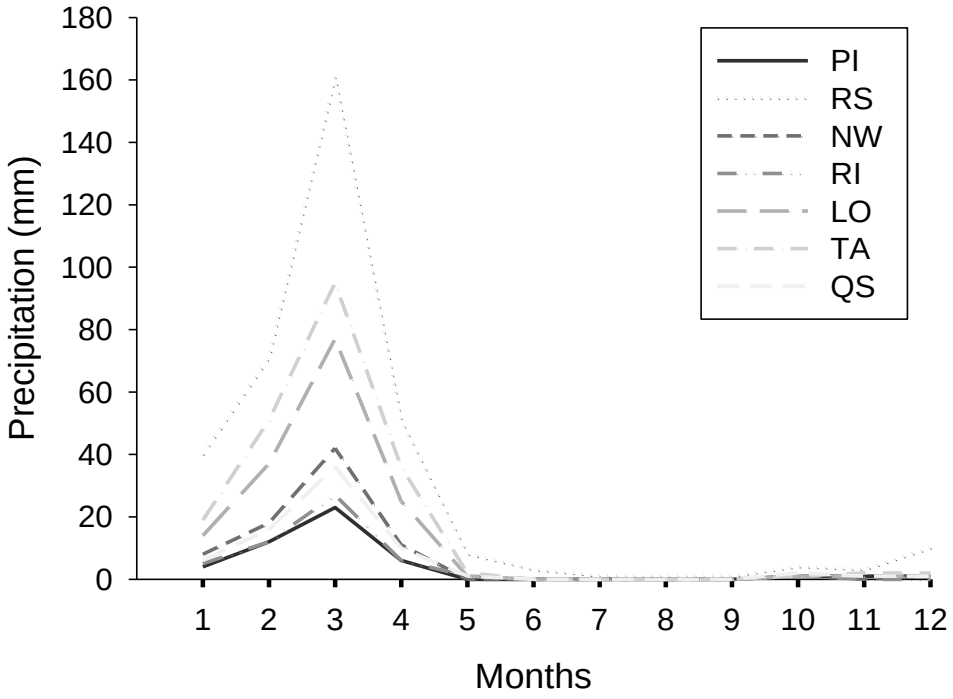


Table A1. Pearson correlation coefficients of all leaf traits at the tree level using log transformed data. **P*<0.05; ***P*<0.01; ****P*<0.001. Bold font means significant values. Abbreviations as in Table 2.

	LDMC	LRWC	A_{mass}	g_s	WUE	Stomatal Density	Abaxial stomatal area	Adaxial stomatal area	LCC	LNC
LMA	**0.55*****	**-0.44*****	**-0.49*****	**-0.34****	0.15	-0.01	0.18	**0.27***	0.10	**-0.28****
LDMC		**-0.51*****	**-0.44*****	**-0.32***	**0.23***	0.05	0.14	**0.26***	0.16	**-0.23***
LRWC			**0.34****	**0.35****	**-0.43*****	-0.1	**0.26***	**0.3****	0.15	**0.19***
A_{mass}				**0.85*****	0.1	-0.07	-0.19	**-0.35***	-0.18	**0.31****
g_s					**-0.28***	-0.07	0.03	-0.15	-0.05	**0.25***
WUE						0.06	**-0.41****	**-0.32***	**-0.22***	-0.11
Stomatal Density							**-0.29***	-0.07	0.04	0.08
Abaxial Stomatal area								**0.4*****	0.18	-0.00
Adaxial Stomatal area									**0.25***	-0.19
LCC										0.11

Figure A3. Pattern of monthly precipitation along the year in each of the studied sites, according to the WorldClim database (1950-2000). Abbreviations for populations as in Table 1.



Capítulo 5

Overcoming edaphic limitations on the dryland forest: The role of soil nutrient concentration on *Prosopis pallida* forest

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Abstract

Dryland ecosystems present low nutrient concentration and poor soil quality that, alongside limited rainfall and high temperature, can restrict plant nutrition and growth. The aims of this research was to know the soil nutrient variability and its effect on plant nutrition of 8 *Prosopis pallida* populations located in a climatic gradient (temperature and precipitation) in the Northern Peruvian dryland forest. We analyzed leaf chemical composition (C, N, P, K, Mg, Ca, Mn, Cu, Zn and Fe) from 15 trees at each population, and used leaf stoichiometry to study plant nutrient uptake. We also measure soil characteristics (texture, pH, electric conductivity and nutrient concentration) at 2 m from each tree. Our results showed that soil nutrient concentrations was not associated with the climatic gradient, and was highly variable within populations. Soil pH was correlated negatively with leaf N/C and P/C, and positively to leaf Ca/C and Cu/C. Soil electric conductivity was positively correlated to leaf K/C and Cu/C, and negatively to leaf Fe/C and Mn/C,. Leaf P/C and Mn/C ratio were related to soil fertility, and it was correlated positively with soil C, N, P, K, and Fe. Leaf Mn/C ratio was negatively correlated with soil C, N, Ca, Mg, Fe, Cu and Zn (7 out of 10 elements studied) and showed significant differences between populations. We conclude that two soil characteristics (pH and EC) were the most relevant to control plant nutrient uptake, especially P uptake, which is also sensitive to soil fertility. Also, our results suggest that leaf Mn/C ratio can be used as an indicator of soil nutrient fertility in *P. pallida* dry forests regardless of the climatic conditions.

Keywords: Variance partitioning; Leaf stoichiometry, Mn; pH; Peru

Introduction

In the harsh conditions of the North Peruvian dryland forest, soil nutrients are scarce, temperature and solar radiation reach high peaks (220 W m^{-2}), and rainfall is below 300 mm (Ffolliott, 1995; Rollenbeck et al., 2015). In these areas, soil texture is generally sandy with low organic matter and low nutrient availability due to extensive leaching of nutrients (Ffolliott, 1995). Aeolian dust transport and deposition of sand particles and leaf litter play an important role

in the soil fertility, increasing nutrient variability (Abril et al., 2009; White et al., 2009). Climatic and edaphic characteristics aggravate the soil poor quality in the Northern Peruvian dryland forests. Soils with high pH decrease the nutrient availability and affects plant growth, while the presence of heavy metal as arsenic, copper or cadmium creates toxic environments for plant development (Alban et al., 2002; Castillo-Michel et al., 2009; Senthilkumar et al., 2005). Additionally, the soil nutrient availability is tightly integrated with the macro-environment (e.g., soil characteristics, climate, and weather) and the regional biota, leading to complex interactions between litter and various ecosystem processes (Cross and Schlesinger, 1999; Ruiz et al., 2008).

Initially, it was believed that this dryland ecosystem was heavily influenced by the El Niño South Oscillation (ENSO). This is an extreme climatic event that increases water availability and create a window of opportunity for tree recruitment and successional communities (Maza-Villalobos et al., 2013; Squeo et al., 2007). This, eventually, led to a significant increase in litter and decomposition that should influence the soil nutrient concentration accordingly. However, recent results suggest that soil characteristics and nutrients could be considered sources of variation, and woody shrub vegetation is controlled by soil pH and K concentration rather than mean temperature or annual precipitation (Muenchow et al., 2013). A similar effect should be found on perennial species, supporting the idea that soil fertility regulates plant nutrition independently of climatic conditions.

Soil characteristics may vary strongly at different ecological scales (Albert, 2015; Lajoie and Vellend, 2015). Thus, differences at population scale would be the result of the variability of climatic and edaphic factors across the environmental gradient, with expected higher soil nutrient concentration in rainy than in arid sites. However, differences at tree and plot scale would be the result of local microclimatic conditions and fertility islands. It is, therefore, interesting to unravel the different sources of soil nutrient variability and its relationship with plant nutrition.

The study of leaf nutrient stoichiometry focuses on the importance of element proportion rather than concentration, and suggests there is an optimal ratio under which an element become limited because of biochemical unbalance in the leaf (Ågren, 2008; Mooshamer et al., 2012). For instance, leaf P/C ratio

is strongly influenced by soil P concentration, and it is correlated positively with ribosomal RNA (Vance et al., 2003). Thus, it is related to plant metabolism, and affect leaf N and C uptake (Schade et al., 2003a; Schreeg et al., 2014). Utterly, leaf stoichiometry can potentially explain nutrient uptake and determine which elements are more relevant in limited ecosystems (Luo et al., 2015).

Under nutrient limitations, roots can develop morphological and physiological changes to increase nutrient mobility regardless of the soil nutrient concentration (Vance et al., 2003). Moreover, roots can exudate malate and citrate to alleviate P deficiency or Al toxicity and increase nutrient uptake (Ryan and Delhaize, 2001). Lambers et al. (2015) suggest that, under low nutrient availability, roots exudate carboxylates to decrease soil pH and increase nutrient mobility, especially P, as wells as other elements like Mn and Fe. Leaf N and P can be retranslocated from old leaves to new leaves, however Mn is retranslocated in low amount as it is stored in the cell vacuole. Thus, leaf Mn concentration can be used as an indicator of plant nutrient uptake strategy and as a functional trait to predict soil nutrient availability (Lambers et al. 2015). Due to the alkaline soils of the dryland forest and restricted climatic conditions, we should expect leaf Mn as a good indicator of nutrient uptake strategy in *P. pallida*.

The Northern Peruvian dryland forests are dominated by *Prosopis pallida* H. et Bonpl. ex Willd. H.B.K. trees (Bravo et al., 2003), hereafter referred as algarrobo, and represent more than 60 % of total plant cover in this ecosystem. Plant growth and tree establishment have been strongly related to climate factors, particularly the El Niño South Oscillation (ENSO) event (Rodríguez et al., 2005; Squeo et al., 2007). However, the relationships of plant nutrient uptake with soil characteristics and nutrient concentration have not been assessed, and these can be an important factor on plant nutrition, especially during the long dry season of the ENSO cycle.

The aim of this study was to understand the role of soil fertility in plant nutrition, and the role of leaf Mn concentration according to soil nutrient concentration and soil characteristics along an aridity gradient in North Peru. This leads to three questions: i) how is soil nutrient variability distributed across this climatic gradient and how much of this variation is caused by population, plot and tree level? ii) How leaf nutrient stoichiometry in *P. pallida* is affected

by soil nutrient concentration? and iii) Can leaf Mn concentration be used to understand plant nutrient uptake strategy in *P. pallida*?

Material y methods

The *Prosopis pallida* dryland forests studied are located between 4º5′ – 6º22′ S and 79º00′ – 81º7′ W in the Piura Province (North-Western Peru, South America; Fig. 1). The geology is characterized by the presence of aeolian or alluvial deposition and topography is characterized by a semi-desertic plain (INRENA 1998). Soil texture present more than 98 % sand, except near the mountain foothill, where silt and clay reach 20 % and 10 % respectively. The altitude varies between 15 and 232 m a.s.l. Even though this zone is located in a tropical area, the Humboldt Current flows through the Pacific coast of Peru and reduces annual precipitation and temperature. The climate is characterized by hot summer and moderated wet winters with a moderate mild annual temperature of 23.4 to 24.8 ºC (Hijmans et al., 2005). Annual precipitation averages between 48 (73 m a.s.l.) and 354 mm (232 m a.s.l.) in summer (January to March), resulting in a long-winter drought of 8-9 months (from April to December) (Bravo et al., 2003). The variation in altitude, temperature, and precipitation indicate the presence of a climatic gradient depending on altitude variation, and increasing from coast the foothills (Fig. 1 and Table 1), while the proximity to the Pacific Ocean also provides a gradient of evapotranspiration decreasing towards inland populations.

Climate variability in this area is highly affected by the El Niño South Oscillation (ENSO), which creates a dry phase of 5-10 years (with the climate conditions described before), and a wet phase of 1-2 years (with an increase in air temperature of 1-2 °C and an increase in annual precipitation up to 2000 mm) (Erdmann et al., 2008).

Soil and leaf samples were taken in summer 2014, during the dry phase of the ENSO cycle. During this period highly stable climatic conditions are found, and monthly temperature variability fit a sine wave with a phase length of one year (Rollenbeck et al., 2015).

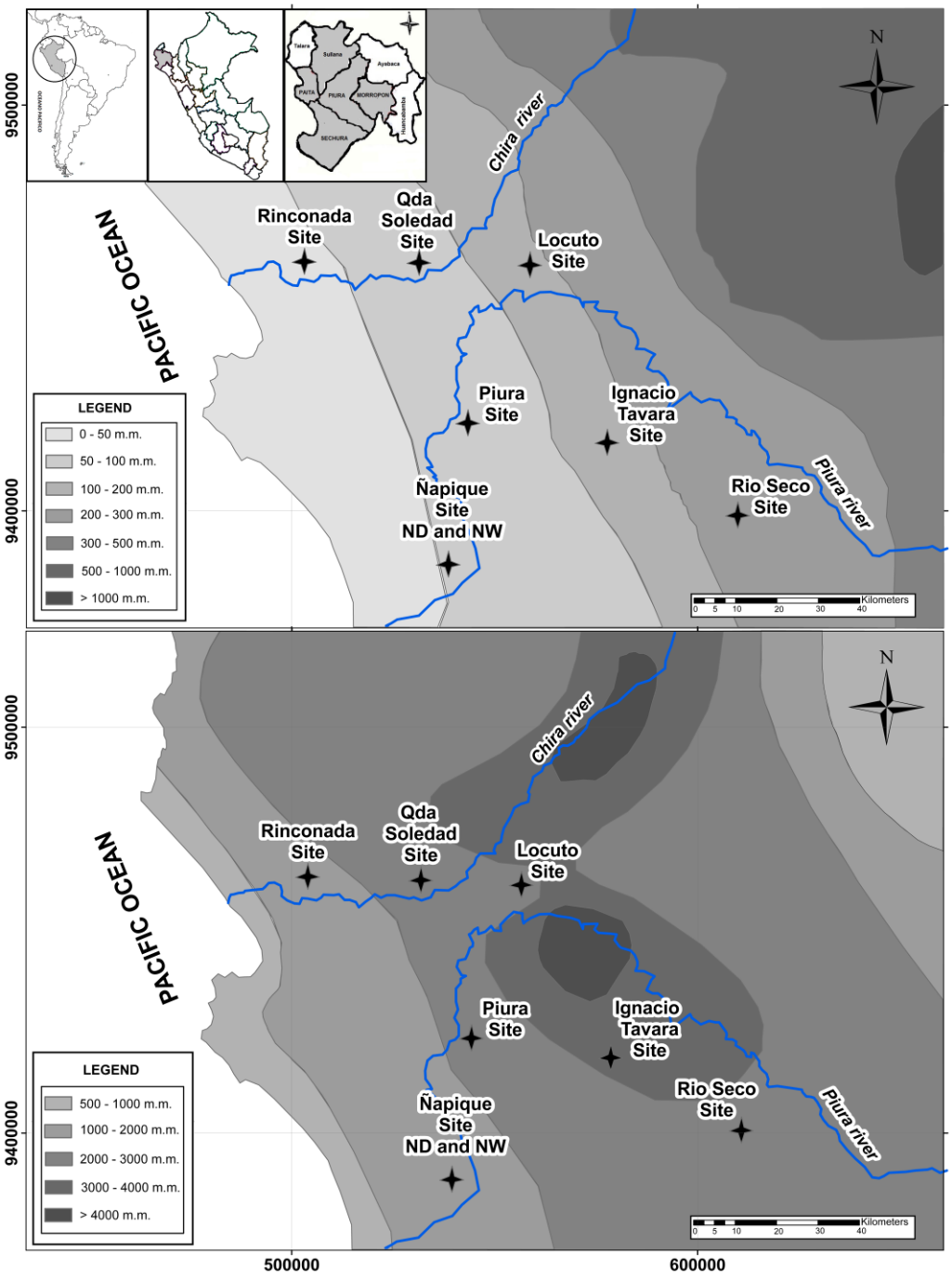

Figure 1. Localization of the eight *Prosopis pallida* populations included in this study. Average rainfall during no-ENSO years (left) and annual rainfall during the 1998 ENSO event (right) across this gradient is shown (adapted from Erdmann et al. 2008).

Sampling design and data collection

Seven *P. pallida* populations were selected to cover the variation in soil characteristics and nutrient concentration, as well as altitude, temperature and precipitation along a climatic gradient (Table 1). Due to one of them (Ñapique) presented high site variability related to the proximity to a lake, this location was considered as two different populations (Ñapique Wet and Ñapique Dry, being the former the closest to the lake). Therefore, we considered a total of eight populations. These locations represent most of the North-Peruvian dryland forest and the plant cover was mainly dominated by *Prosopis pallida* trees. To cover the spatial and microclimatic variability within each site, three plots of ca. 1 ha per population were established. The average distance between plots was 1265 m to avoid pseudo-replication. Within each plot, a random sampling inventory was developed and 5 adult trees of *P. pallida*, with a base stem diameter over 10 cm above the ground, were selected. Individual tree locations were recorded with a real-time differential global positioning system (GPSMAP 76CSx - Garmin USA International, Inc; estimated position error <1 m).

In each tree, a fully expanded, sun-exposed branch was selected and mature leaves with no signs of damages were collected and transported to the lab in hermetic bags to measure leaf nutrient concentration. At 2 m from each tree, soil samples of 25 cm depth were collected to measure soil nutrient concentration as it is described below.

Soil and leaf analysis

Soil and leaf C, N, P, K, Ca, Mg, Cu, Fe, Mn and Zn concentrations were determined. Total C and total N was determined using the LECO method (Wang and Anderson, 1998). Extractable soil P was determined colorimetrically using Olsen method (Olsen et al., 1982). Soil K, Ca, and Mg was determined by ICP-OES, using a 1M NH_4OAc solution at pH = 7. The soil solution is separated from the soil by centrifugation, and the addition of NH_4^+ displaces the rapidly exchangeable alkali and alkaline cations of the soil particles. Soil extractable Mn, Cu, Fe, and Zn were determined by atomic absorption spectrophotometry after digestion using Triethanolamine (TEA) 0.1 M, Diethylenetriaminepentaacetic acid (DTPA) 0.005 M and $CaCl_2$ 0.01 M

(Norvell and Lindsay, 1972). Soil texture was measured in 50 g of soil using the Bouyoucos hydrometer method. Soil pH and electric conductivity (EC) was calculated in 20 g of soil using a portable pHmeter (Hanna hi991301 – Hanna Instruments, Chile).

Statistical analysis

We examined all variables to fit the assumptions of normality and homogeneity of variance, using the Shapiro-Wilk, and Levene test, respectively. When the data did not fit a normal distribution, the data were normalized by $\log_{10}$ transformations. Once the basic requirements were met, a Principal Component Analysis (PCA) between all soil nutrients was used to see the relationship between them and how they are distributed along the different populations. An ANOVA and Tukey HSD post hoc analyses were made using the individual scores of the two main axes of the PCA to determine the significant differences between populations.

To calculate the amount of variation of soil and leaf nutrient concentration explained at each ecological scale (population, plot and tree level), we use the restricted maximum likelihood (REML) method in the lme function of the "nlme" package of R. We fitted a general linear model to the variance across the three scales nested one into another in this increasing order: tree, plot and population.

We calculated leaf nutrient stoichiometry as the ratio of nutrient per C for all nutrients analysed. We explored the relationships of leaf nutrient stoichiometry with soil nutrient concentration and the main two axes of the PCA using Pearson's correlations. Finally, the relationships of leaf Mn/C and soil nutrient concentration within populations were made using a standardized major axis regression of the “smatr” package of R. All statistical analyses were made using R software (R Development Core Team, 2008).

Results

Soil Nutrient variability

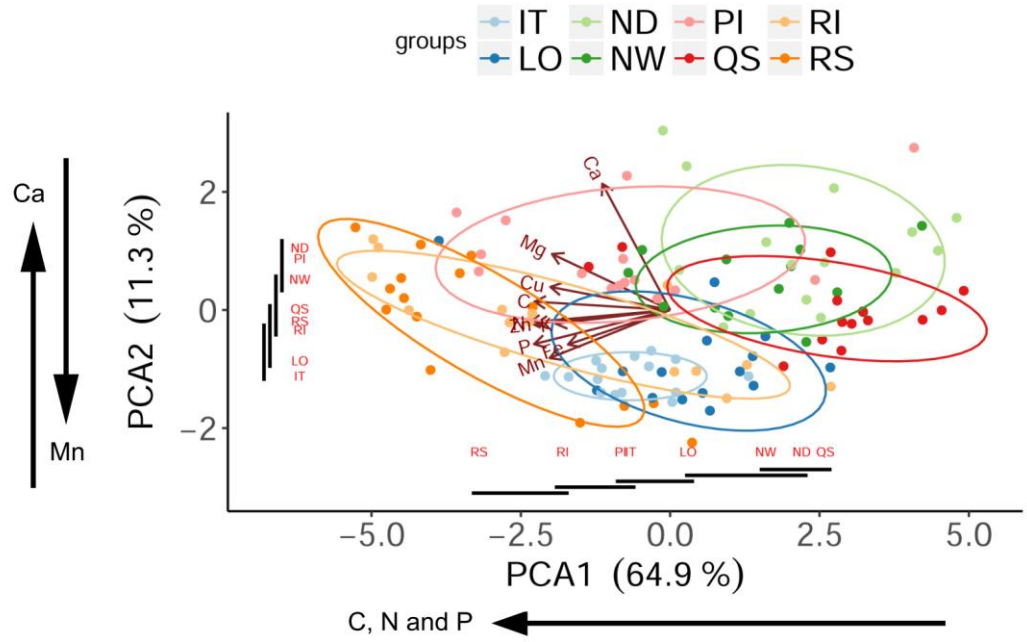

Figure 2. Principal component analysis (PCA) of soil nutrient concentration among all populations. Population score in each axis is shown. Black lines with the population code indicate significant differences between groups of populations (P<0.05) based on the Tukey HSD result. Colored circles grouped population results. See Table 1 for population codes.

The Principal Component Analysis of soil nutrients concentration showed that most of the variability was loaded in the first main axis of the PCA (PCA_1), explaining a 65 % of the total variance, whether the second main axis (PCA_2)only absorbed 11 % of variance (Fig. 2). The first main axis was negatively related to the nutrient concentration of C, N and P, and the second main axis was related to Ca concentration in the positive side and Mn concentration in the negative side (Table S1, Supporting Information).

Soil nutrient concentration showed a wide variation between populations and also a high CV (Table 1). According to the first PCA axis, populations differed in their fertility, from ND and NW with the lowest soil nutrient concentration (being the most dessert-like forests) to RI and RS with the highest

soil nutrient concentration (being the most climate favorable populations). However, no climatic variables correlated with neither axes (data no shown). The two main axes of the PCA were associated to other soil charactherstics as pH and electrical conducitivy (EC). Thus, the PCA_1 was negatively correlated to the soil EC ($r = -0.3$; $P < 0.05$), while the PCA_2 was positively correlated with pH ($r = 0.63$; $P < 0.05$) and soil EC ($r = 0.43$; $P < 0.05$).

Table 1. Soil nutrient concentration, soil characteristics [pH, EC (electric conductivity) and percentage of sand] and climatic characteristics of the studied zones (MAT, mean annual temperature; MAP, mean annual precipitation from the worldClim data [1950-2000]). The coefficient of variation (CV) for each variable is shown in the last column. PI = Piura, RS = Rio Seco, NW = Ñapique wet, ND = Ñapique dry, RI = Rinconada, LO = Locuto, IT = Ignacio Tavara, QS = Quebrada soledad. Mean values (±SE).

	LO	**IT**	**RI**	**RS**	**PI**	**QS**	**NW**	**ND**	**CV**
C (mg kg^{-1})	6.62±1.19	8.87±1.16	13.85±2.67	11.70±1.07	11.44±2.5	3.18±0.78	5.16±0.45	5.13±0.9	82.38
N (mg kg^{-1})	0.71±0.12	0.96±0.11	1.71±0.3	1.49±0.11	1.19±0.24	0.33±0.08	0.48±0.05	0.42±0.07	84.12
P (mg kg^{-1})	16.30±1.9	25.40±1.2	43.58±7.5	34.33±3.7	23.27±2.8	8.72±2.5	5.51±0.9	5.32±1.1	89.9
K (mg kg^{-1})	303±28	429±54	731±85	506±81	449±39	206±34	186±29	202±33	70.69
Ca (mg kg^{-1})	1313±208	1357±45	1865±269	2199±289	3202±294	1380±136	1786±151	2361±386	56.95
Mg (mg kg^{-1})	158±25	146±6	396±68	458±62	176±19	136±20	202±30	168±21	79.41
Fe (mg kg^{-1})	11.69±2.2	13.44±1.1	12.61±2.3	36.76±4.9	4.43±0.5	2.44±0.2	13.90±1.7	8.73±2	100.85
Mn (mg kg^{-1})	12.19±1.5	15.09±0.9	12.95±2	28.95±2.7	8.74±1	7.21±0.7	4.82±0.5	3.86±0.3	78.39
Cu (mg kg^{-1})	0.41±0.12	0.22±0.01	0.42±0.07	1.79±0.23	0.47±0.04	0.20±0.02	0.21±0.01	0.19±0.02	126.13
Zn (mg kg^{-1})	0.47±0.09	0.95±0.11	1.31±0.28	1.65±0.2	2.45±0.42	0.16±0.05	0.16±0.03	0.16±0.04	119.31
pH	6.06±0.16	6.45±0.1	6.51±0.07	6.51±0.15	6.69±0.04	6.82±0.05	6.85±0.04	6.90±0.04	6.11
EC	2.8±0.02	2.73±0.02	3.55±0.2	2.92±0.1	3.03±0.1	2.72±0.04	3.36±0.2	3.36±0.3	21.38
Sand (%)	96.1±0.5	95.0±0.8	97.3±0.7	62.9±6.3	95.6±0.6	96.8±0.4	97.4±0.4	96.7±0.9	14.44
MAT	24.3	24.8	23.4	23.2	23.9	23.9	23.7	23.7	1.98
MAP	157	208	52	354	48	73	81	81	83.7

Soil and leaf variability at different scales

The variance partitioning analysis showed that soil nutrient variability was equally distributed among population (38 %), plot (23 %) and tree (39 %) level (Fig. 3). However, excluding some trace elements (Fe, Cu and Mn), explained variance was higher at plot and tree level (71 %) than population level (29 %). These differences were even higher in the variance partitioning of the leaf nutrient concentration, showing a 73 % of variance explained at plot and tree level, indicating a higher importance of local factors (Fig. 3).

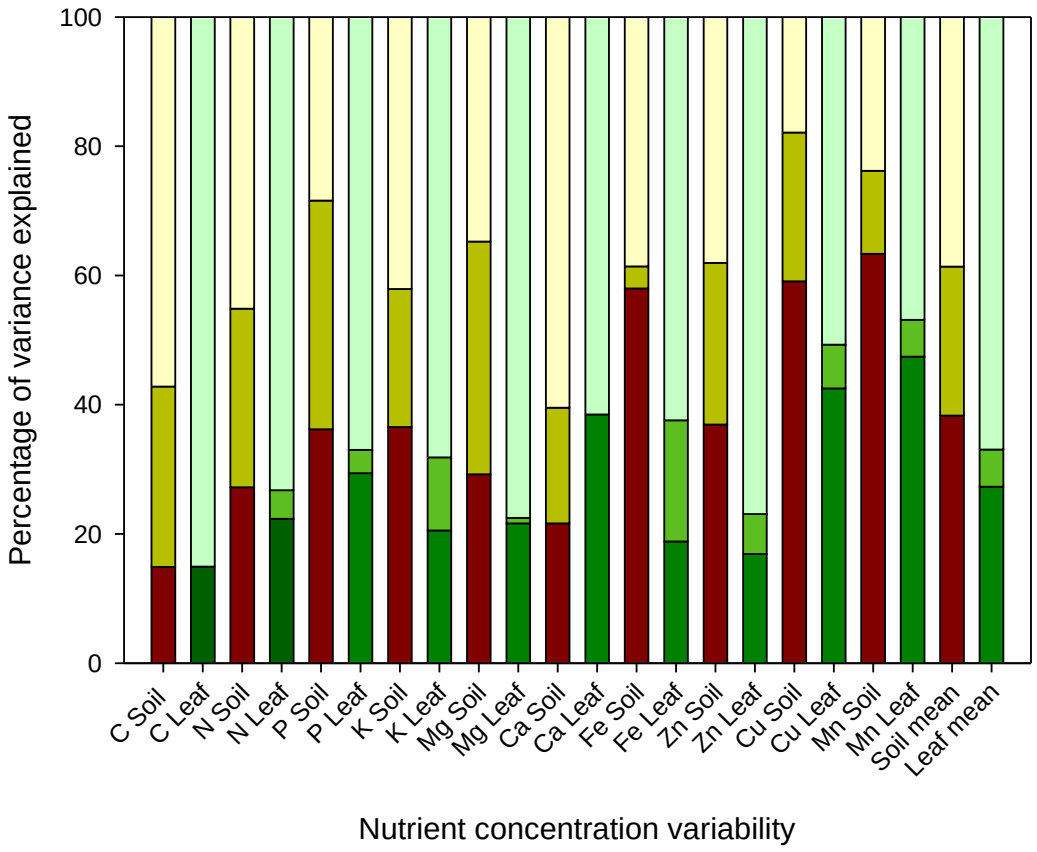

Figure 3. Soil and leaf nutrient variability at different ecological scales (population, plot and tree). Brown, olive green, and yellow represents the percentage of variance explained for soil nutrients at population, plot and tree level, respectively. Dark green, green, and light green represents the percentage of variance explained for leaf nutrients at population, plot and tree level, respectively

Leaf stoichiometry – soil nutrient relationships

Table 2. Correlation between leaf nutrient stoichiometry (log transformed) and pH, soil nutrient concentration (log transformed). Correlation coefficient and significance level is shown (*P < 0.05, **P < 0.01). PCA_1 and PCA_2 are the two main axes of the PCA. n = 112

		Leaf nutrient stoichiometry								
		N/C	P/C	K/C	Ca/C	Mg/C	Fe/C	Mn/C	Cu/C	Zn/C
pH		**-0.21***	**-0.30****	-0.02	**0.23***	0.09	-0.02	-0.09	**0.26****	-0.11
EC		0.07	0.12	**0.25****	-0.07	0.03	**-0.27****	**-0.33*****	**0.24****	0.06
PCA1		-0.14	**-0.18***	-0.05	0.13	-0.01	-0.01	**0.21***	0.17	-0.06
PCA2		-0.08	-0.15	0.07	0.05	-0.05	-0.14	**-0.27****	**0.39*****	-0.04
Soil nutrient content (mg kg^{-1})	C	0.10	**0.18***	0.07	**-0.19***	-0.06	0.02	**-0.25****	-0.13	0.00
	N	0.13	**0.20***	0.08	**-0.19***	-0.04	0.02	**-0.24****	-0.15	0.03
	P	0.17	**0.20***	0.05	-0.08	0.04	0.05	-0.05	**-0.27****	0.08
	K	0.14	**0.19***	0.06	-0.01	0.05	0.04	-0.05	-0.15	0.08
	Ca	-0.02	-0.06	0.03	0.00	-0.06	-0.05	**-0.26****	0.16	-0.04
	Mg	0.06	0.10	0.09	-0.01	0.11	-0.10	**-0.28****	0.05	0.02
	Fe	-0.01	**0.18***	-0.06	-0.17	-0.02	0.03	**-0.26****	**-0.27****	-0.09
	Mn	0.16	0.13	-0.08	0.00	0.15	0.11	0.10	**-0.36*****	0.05
	Cu	0.16	0.10	0.05	-0.12	0.00	-0.09	**-0.27****	0.03	0.13
	Zn	0.17	**0.18***	0.07	**-0.18***	-0.11	0.02	**-0.19***	-0.19	0.14

Leaf stoichiometry showed some significant correlations with soil characteristics. For example, pH correlated positively with leaf N/C and P/C ratio and negatively to leaf Ca/C and Cu/C ratio. Soil EC correlated positively with leaf K/C and Cu/C ratio, and negatively with leaf Fe/C and Mn/C ratio (Table 2). The PCA_1 (negative values representing more fertility sites) was correlated negatively with the leaf P/C ratio and positively with leaf Mn/C ratio. The PCA_2 (associated to an increase in pH) was correlated positively with the leaf Cu/C ratio and negatively with leaf Mn/C ratio (Fig. 4). Moreover, P and Mn leaf stoichiometry showed significant correlations with the soil nutrient concentration. Similarly as it has been shown by the PCA analyses, leaf P/C ratio was correlated positively to soil C, N, P, K and Fe concentration (fertility gradient), while leaf Ca/C was correlated negatively with soil C, N, and Zn concentration. Leaf Cu/C ratio was negatively correlated with soil P, Fe, Mn, and Zn concentration (Table 2).

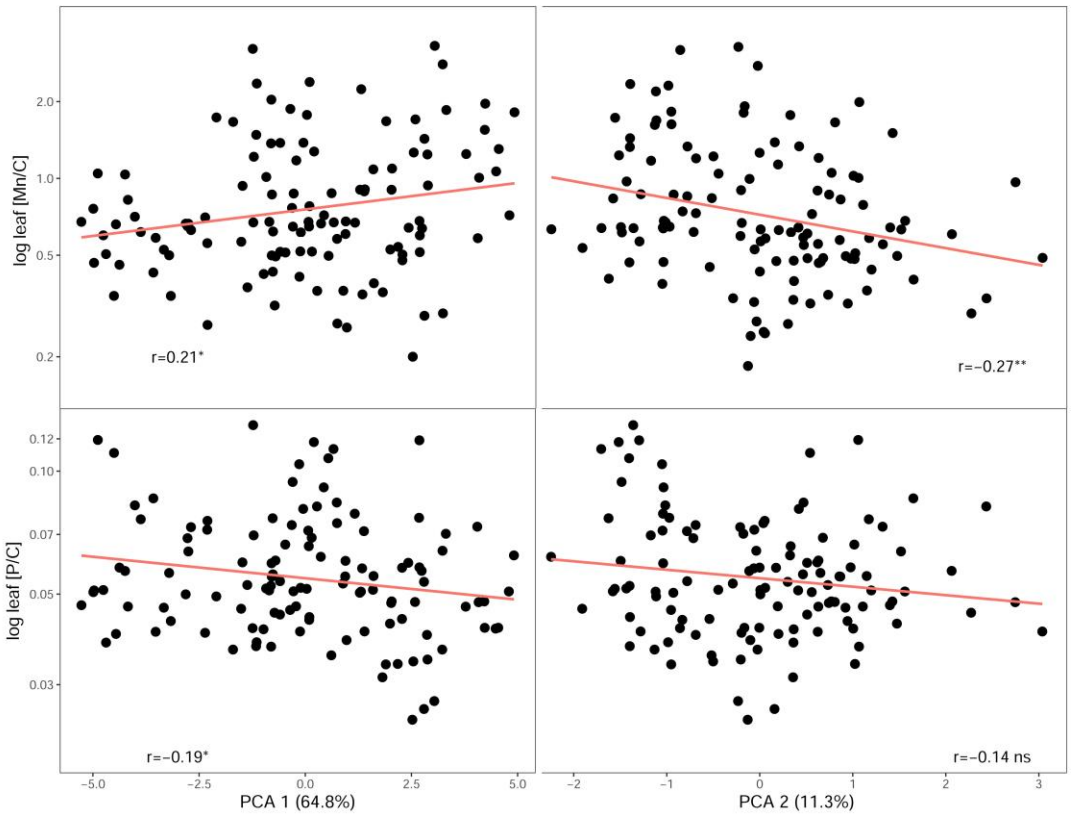

Figure 4. Relationships between leaf Mn/C, leaf P/C ratio, PCA1 and PCA2. Correlation coefficient and significance level is shown (*P < 0.05, **P < 0.01). n = 112.

Special attention should be paid to the leaf Mn/C ratio, which was negatively correlated to soil C, N, Ca, Mg, Fe, Cu and Zn concentration (7 of the 10 elements studied).

Leaf [Mn] – soil nutrient relationships

Similar correlations were found considering the leaf Mn concentration instead of leaf Mn/C. Thus, in order to study the potential of leaf Mn as an indicator of soil nutrient mobility and/or soil fertility, we used leaf Mn concentration instead of leaf Mn/C. Leaf Mn showed significant negative correlations with most of the soil nutrients (Table 3 and Fig. 5). However, most of these relationships were not significant within populations. Leaf Mn in PI (the population with trees more homogeneous, see below) showed significant negative correlations with most soil nutrients (Table 3). For the essential nutrients (C, N and P), the slope of these relationships were lower in PI than in the regional pool, while the two most dessert-like forests (NW and ND) showed

a more negative slope of leaf Mn/C and soil N, and leaf Mn and soil Zn (Fig. 6).

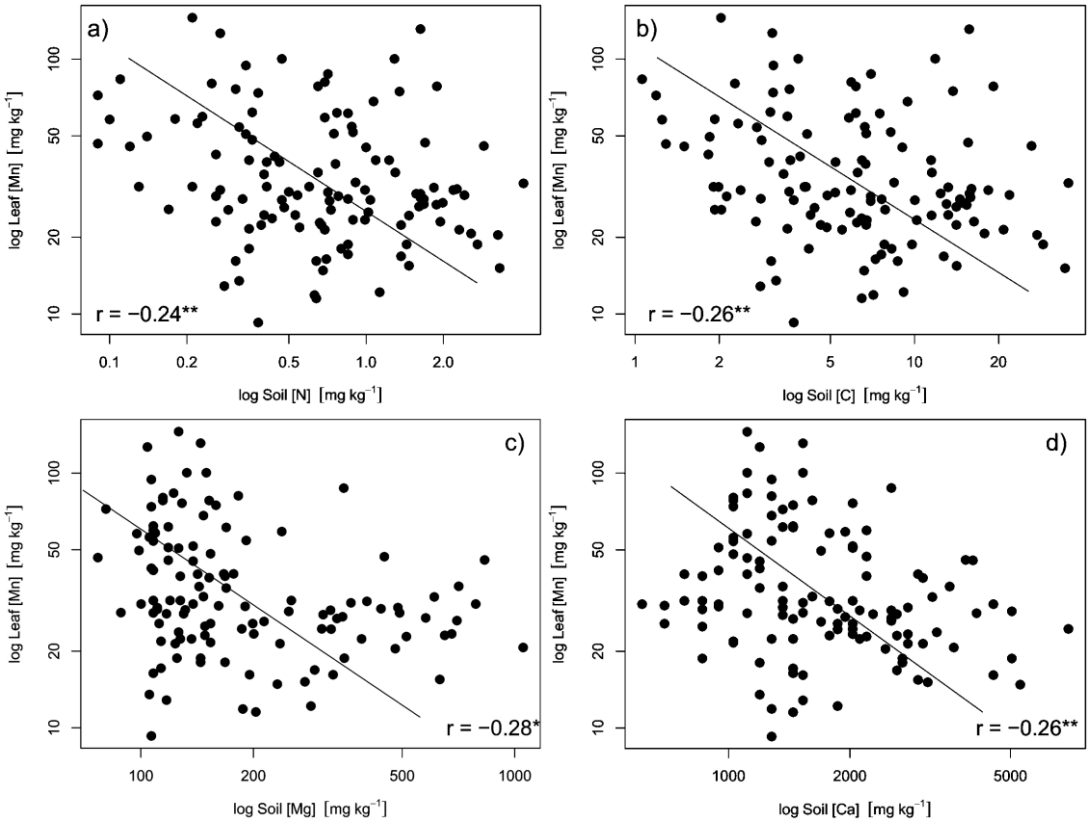

Figure 5. Relationships between leaf Mn concentration and soil N (a), C (b), Mg (c) and Ca (d) concentration. Correlation coefficient and significance level is shown (**P* < 0.05, ***P* < 0.01). n = 112

Table 3. Standardized Major Axis (SMA) regressions for evaluation of the relationships of leaf manganese (Mn) with soil nutrients, for the total pool (n = 112) or for the different study sites (n = 15). The value of the regression slope (the scaling exponent from major axis regression) and significance level ([a] *P*<0.07, **P* < 0.05, ***P* < 0.01) is also shown.

log (10)	log (10)	Total Pool	Study site							
X	Y	n (112)	RS	RI	PI	IT	LO	NW	ND	QS
[Mn]	[C]	**-0.69****	0.89	-0.31	**-0.45***	0.78	0.44	1.29	**-0.35[a]**	-0.85
[Mn]	[N]	**-0.65****	1.21	-0.33	**-0.45[a]**	0.85	-0.46	-1.21	**-0.88***	-0.75
[Mn]	[P]	-0.54	-0.65	-0.35	**-0.47[a]**	1.99	-0.54	-0.68	-0.78	-0.81
[Mn]	[K]	-0.76	0.44	-0.61	**-0.87***	-0.80	-0.76	-0.76	1.13	-0.98
[Mn]	[Ca]	**-1.14****	-0.57	-0.47	-1.1	-2.94	-0.75	**1.49[a]**	1.26	**1.80[a]**
[Mn]	[Mg]	**-0.99****	0.50	-0.45	**-0.98[a]**	-2.40	-0.74	-0.95	-1.36	-1.35
[Mn]	[Mn]	0.78	0.95	-0.55	-0.67	1.89	-0.92	-1.39	-1.92	-1.65
[Mn]	[Cu]	**-0.88****	-0.56	-0.55	**-1.00****	3.2	0.44	-1.9	-1.68	-1.89
[Mn]	[Fe]	**-0.58****	0.60	-0.42	-0.67	-1.07	-0.44	-1.14	-0.63	-1.69
[Mn]	[Zn]	**-0.39***	0.62	-0.25	**-0.48[a]**	-0.87	-0.47	**-0.45[a]**	**-0.51***	-0.46

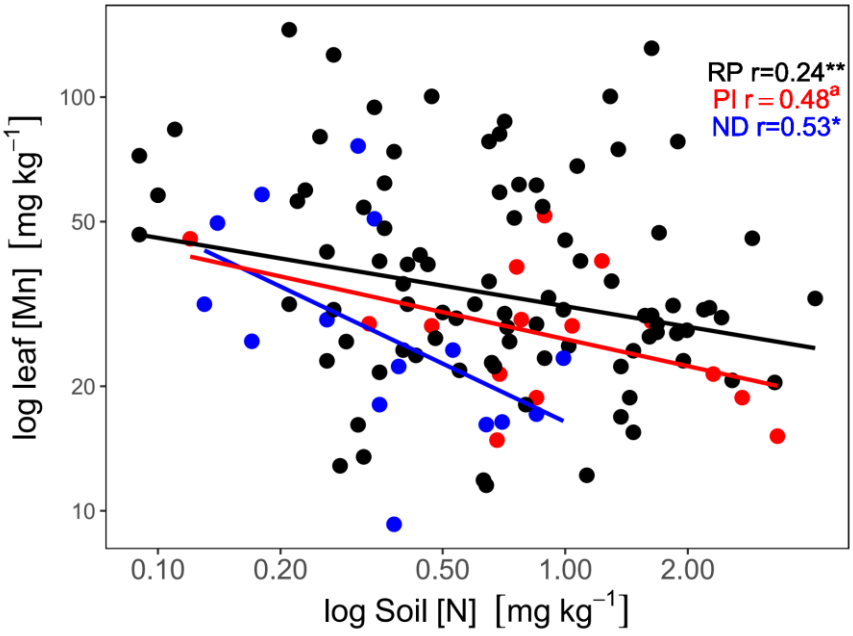

Figure 6. Relationships between leaf Mn concentration and soil Nitrogen concentration between populations. The linear regression of the Regional Pool (RP - black line), PI population (red line) and ND population (blue line) is shown, as well as the correlation coefficient and significance level (^{a} P<0.07, *P < 0.05, **P < 0.01).

Discussion

Soil nutrient concentration across the Northern Peruvian dryland forest showed a high variability. Most of these variations were located within each population (at tree and plot level). Soil chemical characteristics (as pH and EC) played an important role in leaf stoichiometry. Leaf macronutrients (N and P) were correlated negatively with pH, while micronutrients like Fe and Mn were correlated negatively with EC. Leaf Mn/C ratio was a good indicator of soil nutrient concentration, and it was correlated negatively with 7 of the 10 soil nutrients studied. Differences between populations suggest that higher amounts of leaf Mn can be accumulated in dessert-like populations under low soil fertility.

Soil Nutrient Variability

Soil nutrient concentration showed clear relationships between them with more than 60 % of all variance absorbed by the PCA_1 axis. The PCA_1 was negatively correlated with soil EC, and followed a fertility gradient that it is not related to the climatic conditions. The lowest soil nutrient concentration was located in NW and ND populations (in the Sechura dessert), while the highest

values were located at RI and RS populations. RI coastal location present a shallow underground water and low evapotranspiration due to cold winds from the Pacific Ocean that could increase leaf litter decomposition and soil respiration; influencing, ultimately, the high soil nutrient concentration (Fang et al., 2015; White et al., 2009). RS, located in the far foothills, presents more silt and clay soil texture, which increases cation exchange capacity and may explain the high concentration of trace elements (Cu, Mn and Fe) in this location. Utterly, this suggests that the soil fertility gradient is an independent factor and can be considered a force of variation on its own. The PCA_2 was highly correlated with both soil pH and CE, therefore soil chemical characteristics are also influencing soil nutrient variability across this region.

Despite the tight relationship between soil nutrients, we found a high amount of variation explained at tree and plot level (except for Fe, Cu and Mn). This can also be seen in the results of the PCA and suggest that the variability whitin locations is stronger than between them. This is a common feature in dryland ecosystems and it is enhanced by a patchy vegetation cover and a high spatial variation of soil processes as respiration (Liu et al., 2016; Puigdefábregas, 2005). *Prosopis* has been recognized as a fertility island tree that significantly increase soil nutrient concentration under its canopy, and improve soil microbial activity and diversity (Abril et al., 2009; Vallejo et al., 2012). Moreover, the highest amount of variation of leaf nutrient concentration was explained at tree level, which could be due to the soil heterogeneity at small scale (Cross and Schlesinger, 1999). This supports the idea that soil nutrient variability can change significantly at short distances as a result of the sparse vegetation cover and its effect on soil nutrient cycle.

Effect of soil chemical characteristics and soil fertility on plant nutrient uptake

The soil fertility gradient and the soil chemical characteristics showed a strong effect in leaf nutrient stoichiometry. The PCA_1 (negative values representing more fertile sites) was correlated negatively with leaf P/C ratio, thus more fertile soils have a higher leaf P/C ratio. Recent studies have shown that P is a more limiting element than N in tropical forests (Hedin, 2004; Paoli et al., 2005), and alongside soil pH, can be largely more important than climatic conditions (Maire et al., 2015). Phosphorous is a macronutrient involved in

several biochemical molecules and physiological process, thus an increase in leaf P/C should be associated with the uptake of several macronutrient and trace element rather than only soil P (Schade et al., 2003b). Therefore, leaf P uptake will be limited by soil fertility. Additionally, the PCA_2 and leaf P/C ratio were negatively correlated with soil pH, and even though this two variables did not correlated together, we found a negative trend that support the fact that soil P can be limited in the alkaline conditions. This relationship has been heavily documented, soil pH controls the form in which inorganic P exist in the soil solution, and it should be higher at soil pH between 5 to 6 (Schachtman et al., 1998). It has been suggested soil pH can be modified locally to increase P mobility under low nutrient concentrations (see below) (Lambers et al., 2015). Mn mobility is also enhanced through this process, therefore, this may explain the relationship between the PCA_2 and leaf Mn/C ratio. Ultimately, our results indicate that soil P concentration is a limited nutrient for algarrobo in the dryland forest, and it is affecting nutrient uptake as whole. Also, it suggests that leaf Mn concentration can be used to trace soil fertility and nutrient mobility.

Soil EC correlates positively with PCA_2, leaf K/C and leaf Cu/C, and negatively with the PCA_1, leaf Fe/C and Mn/C ratio. Soil EC is directly related to cation exchange capacity, water-holding capacity and soil porosity (Rhoades and Chanduvi, 1999; Smith and Doran, 1996). Thus, high soil EC increases trace element accumulation and plant uptake (Officer et al., 2004), and thefore it i is associated with soil fertility. High soil EC is related to a lower leaf Mn uptake, because soil nutrient mobility under high soil EC is based on soil nutrient fertility, rather than local soil characteristic changes that could increase leaf Mn uptake. Similar results suggest soil EC can be a driver of species distribution in this dryland forest independently of the precipitation gradient (Muenchow et al., 2013). Therefore, this result confirm that soil EC is important soil characteristic related to both soil fertility and plant nutrient uptake even within the same species.

Under relatively high pH, we found a significant increase in leaf Ca/C ratio, which is a biological signal of soil nutrient deficiency, drought and salt stress (Cheong et al., 2003). Similarly, we found a negative relationship between leaf Ca/C ratio and soil C, N and Zn concentration, supporting the idea that leaf Ca accumulation is a physiological response to soil nutrient deficiency

or lack of mobility. Leaf Cu/C ratio, on the other hand, should be address independently because algarrobo can accumulate this element and other heavy metals easily (Gardea-torresdey et al., 2005; Senthilkumar et al., 2005). The negative correlation of leaf Cu with soil P, Fe and Mn may be explained because Cu uptake is sensitive to soil chemical characteristics, especially pH (Sauvé et al., 1997; Temminghoff et al., 1997).

Leaf Mn as an indicator of soil nutrient availability

A local decrease in soil pH by root carboxylate exudation in low nutrient environments could increase plant nutrient uptake, particularly P alongside Mn (Lambers et al. 2015). This effect is stronger in non-mycorrhizal species than in mycorrhizal species (like algarrobo) because the latter access to more nutrients through symbiosis. However, we already found that pH was strongly affecting leaf stoichiometry, especially leaf P. Low soil water availability and high temperature could decrease soil microbial activity, especially in dry ecosystems (Cable et al., 2011; Thomas et al., 2011), reducing the uptake of P by mycorrhiza, as well as C and N (Delgado-Baquerizo et al., 2013). Thus, one mechanism of roots of *P. pallida* to increase soil nutrient availability could be to exudate carboxylates to decrease pH. We found that leaf Mn/C was negatively correlated with soil C, N, Ca, Mg, Fe, Cu and Zn; which confirm that leaf Mn uptake increases under low soil nutrient availability. Despite this, there was no significant correlation between leaf Mn/C ratio and soil P or pH, which does not support the idea that leaf Mn can be used as an indicator of nutrient mobility, at least in the case of soil P. The lack of correlation between leaf Mn and soil P is a concern and could be the result of high variability between samples due to leaf age or plant size, or differences in soil EC, which also affect Mn uptake (Zhang et al., 2013).

In most cases, there were no significant relationships between leaf Mn and soil nutrient concentration within populations. This could be since the sample number within population was too low (n=15) and soil variability in this ecosystem is too high. Regardless, we found significant relationships between leaf Mn and soil C, N and Zn in ND population, the driest and poorest nutrient soil location. This result supports the hypothesis that root activity controls

nutrient availability in low nutrient habitats (Lambers et al., 2015). We also found several significant relationships in PI population, and this is probably because it is the only *P. pallida* plantation, where trees have averagely the same age, grazing is very low and pruning is scheduled to improve plant growth. Thus, the reduction of external sources of variation may reinforce the relationships between leaf and soil nutrients (Ågren, 2008; Mooshamer et al., 2012). This result points out that leaf Mn can be used to trace soil nutrient mobility, however, it is highly affected by the natural high variability of dry ecosystems.

The relationships between leaf Mn and soil N concentrations showed significant differences in elevation and slope in PI and ND populations. Leaf Mn was lower in PI than in ND, and this was clearly related to the higher soil N concentration in PI than in ND. A shift in leaf stoichiometry was also found in very severe drought conditions, similar to those found ND desert-like forest (Urbina et al., 2015). Moreover, we found a significant shift in slope; therefore, a decrease in soil N concentration produces a higher increase in leaf Mn concentration in ND than in PI (Fig. 5a) and it can be explained by the lower soil nutrients and higher soil pH in ND than in PI. Utterly, this shows that the relationship between leaf Mn and soil nutrient concentration can be used to study plant nutrition based on soil fertility and its chemical characteristics.

Conclusions

Despite the high temporal variability of climatic factors in the North Peruvian dryland forest due to the ENSO phenomenon, soil nutrient concentration does not follow any climatic gradient and most of its variability is local (at plot and tree level). Instead, it shows a strong fertility gradient that does not follow any climatic or geographic gradient and thus, can be consider a source of variation on its own. Soil characteristics and soil nutrient concentration have a strong effect on plant nutrient uptake and then on leaf nutrient stoychiometry. Leaf P/C and Ca/C ratio were related to the soil fertility and soil pH. Leaf Mn concentration was correlated negatively with 7 out of 10 soil nutrients studied, and a high amount of leaf Mn is accumulated in unfertile and alkaline soils. Thus, it can be used as a proxy for soil nutrient fertility.

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Supporting information

Table S1. Variable scores for the two main axes of the principal component analysis (PCA_1 and PCA_2).

	PCA_1	PCA_2
C (mg kg^{-1})	**-0.91**	0.06
N (mg kg^{-1})	**-0.94**	-0.08
P (mg kg^{-1})	**-0.91**	-0.23
K (mg kg^{-1})	-0.76	-0.09
Ca (mg kg^{-1})	-0.45	**0.85**
Mg (mg kg^{-1})	-0.79	0.38
Fe (mg kg^{-1})	-0.68	-0.23
Mn (mg kg^{-1})	-0.80	**-0.32**
Cu (mg kg^{-1})	-0.80	0.16
Zn (mg kg^{-1})	-0.89	-0.09

Capítulo 6

Fertility island effect in *Prosopis pallida* is dependent of tree size, leaf structural and chemical traits

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Abstract

Trees provide a significant increase in soil nutrients, water availability, and soil microbial activity in many ecosystems. In arid ecosystems, these species creates “fertility islands” that increase biodiversity and plant life around them. The fertility island effect in *Prosopis* sp. has been long recognized in the dryland forests despite their sandy soils, limited rainfall and low soil nutrient concentration. In this study, we assess the fertility island effect of *Prosopis pallida* in the North Peruvian dry forest, and analyze if it is influenced by plant size and structural and/or chemical leaf traits. We measured the soil nutrient concentration of soil samples at 2, 4, 6, and 8 m distance from the tree base in 40 trees belonging to five populations that differ in mean annual temperature and annual rainfall. We also measured tree size (height, stem diameter, and crown area), leaf structure (leaf mass per area and leaf dry matter content), and leaf nutrient composition (C, N, P, Cu, Fe, Mn and Zn). Our results showed that soil fertility increased under the tree canopy for all the nutrients except Cu and Zn. Plant size, leaf structure and nutrient composition affect significantly the soil C, N, P and Mn concentration. Moreover, when these beneficial plant traits combine with favorable climatic conditions and acid soil pH, it can create a stronger fertility island effect, improving soil fertility despite the water limitations.

Keywords: algarrobo, leaf traits, LMA, nitrogen, soil respiration, tree size

Introduction

In the harsh conditions of the dryland forest, soil nutrients are limited, temperature and solar radiation reach high values, and rainfall is lower than 300 mm (Ffolliott, 1995; Vásquez-Méndez et al., 2010). Several N-fixing species are able to survive under the harsh conditions of the dryland forest and improve soil nutrient concentration (Ruiz et al., 2008; Simmons et al., 2008). *Prosopis* sp. has been widely studied as a “soil conditioner“, showing a positive effect on soil N, K and P concentration (Herrera-Arreola et al., 2007), microbial activity (Reyes-Reyes et al., 2007, 2002), and relative humidity under its canopy (Abril et al., 2009). The significant improvement in soil quality has been called "fertility island", and creates a microhabitat where microbial organisms, insects, plants and mammals found shelter (Catenazzi

and Donnelly, 2007; Forbes et al., 2005; Zavala-Hurtado, 2000). This improvement is the result of a continuous input of organic material and an active microbial decomposition process (Ruiz et al., 2008). Thus, soil microbial diversity and soil respiration have been found to be higher under the *Prosopis* canopy (Hollister et al., 2010; Ruiz et al., 2008).

Alongside the organic input that comes from leaf litter, other factors boost nutrient availability and biodiversity below *Prosopis* trees. Tree canopy, for instance, reduces solar radiation, temperature, and evapotranspiration (Berry et al., 2013). Thus, it provides a suitable environment for microbial colonization (Vallejo et al., 2012). This, next to root exudates, promotes microbial activity, which is also positively affected by the tree size (Curiel Yuste et al., 2007; Wang et al., 2014). These changes in the soil environment also create better conditions for seed germination below the tree canopy (Bashan et al., 2000). However, there is a significant reduction of radiation which diminishes the number of species capable to germinate. Thus, it is more common to find fungi species under the canopy, and shade tolerant species (Linares-Palomino and Alvarez, 2005; Purohit et al., 2002).

Other characteristics can affect the fertility island effect as the plant size, leaf structure, and leaf nutrient composition. For example, the low leaf nutrient concentration in *P cineriana* and *P. caldenia* has been related to the small effect of tree cover on soil nutrient concentration (Buschiazzo et al., 2001; Deans et al., 2003). While in *P. laevigata* and *P. flexuosa,* higher trees with higher leaf nutrient concentration provide more nutrient input into the soil (Abril et al., 2009; Reyes-Reyes et al., 2007). Therefore, the study of the tree size and leaf nutrient composition provides a new insight to understand the fertility island effect in dryland ecosystems.

Significant increments of soil N and organic C concentration have been found in most cases but rarely for P and K. This showcase the differences in plant-soil dynamics between species and ecosystems. For instance, *P. chilensis* is capable to increase soil P and K concentration in Senegal, unlike *P. juliflora* or *P. Cineraria* (Deans et al., 2003). However, *P. chilensis* have shown to reduce soil P in Kenya dryland forest (Kahi et al., 2009). Less effort has been made to determine the impact of *Prosopis* on other elements as Ca, Mg or Fe (Whitford, 2002), even though it have shown to accumulate heavy metals in *P. laevigata* and *P. juliflora* (Buendía-González et al., 2010;

Senthilkumar et al., 2005). The significant effect of Prosopis is stronger under the tree canopy, and diminish gradually up to the intercanopy space creating a fertility gradient towards the tree base (Qi et al., 2010). This effect also contribute to increase the soil nutrient variability in the dryland forest and perpetuate the patchy structure of this ecosystem.

Vegetation composition in the North Peruvian dryland forest are mostly controlled by the Humboldt Current and the El Niño Southern Oscillation (ENSO), which creates dry long periods and short rainy events. The lack of precipitations during the dry season suggest that soil fertility could be an important driver of plant growth and diversity in this ecosystem (Muenchow et al., 2013). In the Peruvian dryland forests, *Prosopis pallida* is the dominant species and represents 61% of the plant cover in this area (Bravo et al., 2003). Even though we might expect that the effect of *P. pallida* in soil fertility could be similar to other *Prosopis* species, the periodical presence of the ENSO and the species high genetic variability might produce a different pattern of litter decomposition and therefore of the fertility island effect. Microbial activity, leaf productivity, and nutrient mobilization face seasonal dynamics in this area, which increase after rainfall events and decrease during the long dry period (Abril et al., 2009; Curiel Yuste et al., 2007; Ruiz et al., 2008). Climatic variability in this ecosystem could significantly affect *P. pallida*, and utterly the fertility island effect. Thus, it is possible that the fertility island effect is not present under no-ENSO conditions and/or may be affected by these climate conditions or local characteristics.

The aim of this research was to assess the fertility island effect under *P. pallida* canopy, and its relation with tree size and leaf traits along an aridity gradient in North Peru. It is hypothesized that tree size and leaf traits would be linked to soil nutrient concentration, and they would be more relevant in less arid locations explaining the higher nutrient availability in wetter sites. Ultimately, this leads to three questions: i) is the fertility island effect related to the distance from the tree stem?; ii) It is this effect associated to plant size and leaf functional traits?; and iii) it is this effect different among populations differing in climatic and/or edaphic factors?

Material and Methods

The *Prosopis pallida* dryland forests studied are located between 4º5′ – 6º22′ S and 79º00′ – 81º7′ W in the Piura Province (North-Western Peru, South America; Fig. 1). The study area consists mainly of forests, the principal species of which is *Prosopis pallida*, (Humb. & Bonpl. ex Willd.) Kunth (algarrobo), accompanied by *Loxopterygium huasango* Spruce ex Engl. (hualtaco), *Bursera graveolens* (Kunth) Triana and Planch. (palo santo), and *Capparis angulata* R. & P. (sapote) in the tree stratum. The geology is characterized by the presence of aeolian or alluvial depositions with more than 98% sand texture. The topography is characterized by a semi-desertic plain (INRENA 1998),. The altitude varies between 15. and 153 m a.s.l. The area has a semi-arid climate characterized by hot summers and moderated wet winters with a moderate mild annual temperature of 23.4 to 24.8 ºC. Annual precipitation averages between 52 (92 m a.s.l.) and 208 mm (153 m a.s.l.) in summer (January to March), resulting in long-winter droughts (Bravo et al., 2003; Hijmans et al., 2005). These dry conditions are normally interrupted by the ENSO phenomenon, which increase summer precipitation up to 10 folds, and summer temperature up to two degrees (wet season). The last ENSO phenomenon was in 1998. After that, the area has faced a significant increase in temperature (up to 25-26 °C in summer) and minimal precipitation (3.4 – 83.1 mm), creating harsh conditions during this long no-ENSO period (Harris et al., 2014). Altitude, temperature, and precipitation variation from the cost to inland indicates the presence of a rainfall gradient increasing from west to east (Fig. 1 and Table 1). Moreover, the standardized precipitation-evapotranspiration index (SPEI) indicates that inland populations present drier conditions than coastal populations regardless of the rainfall gradient (Beguería et al., 2014).

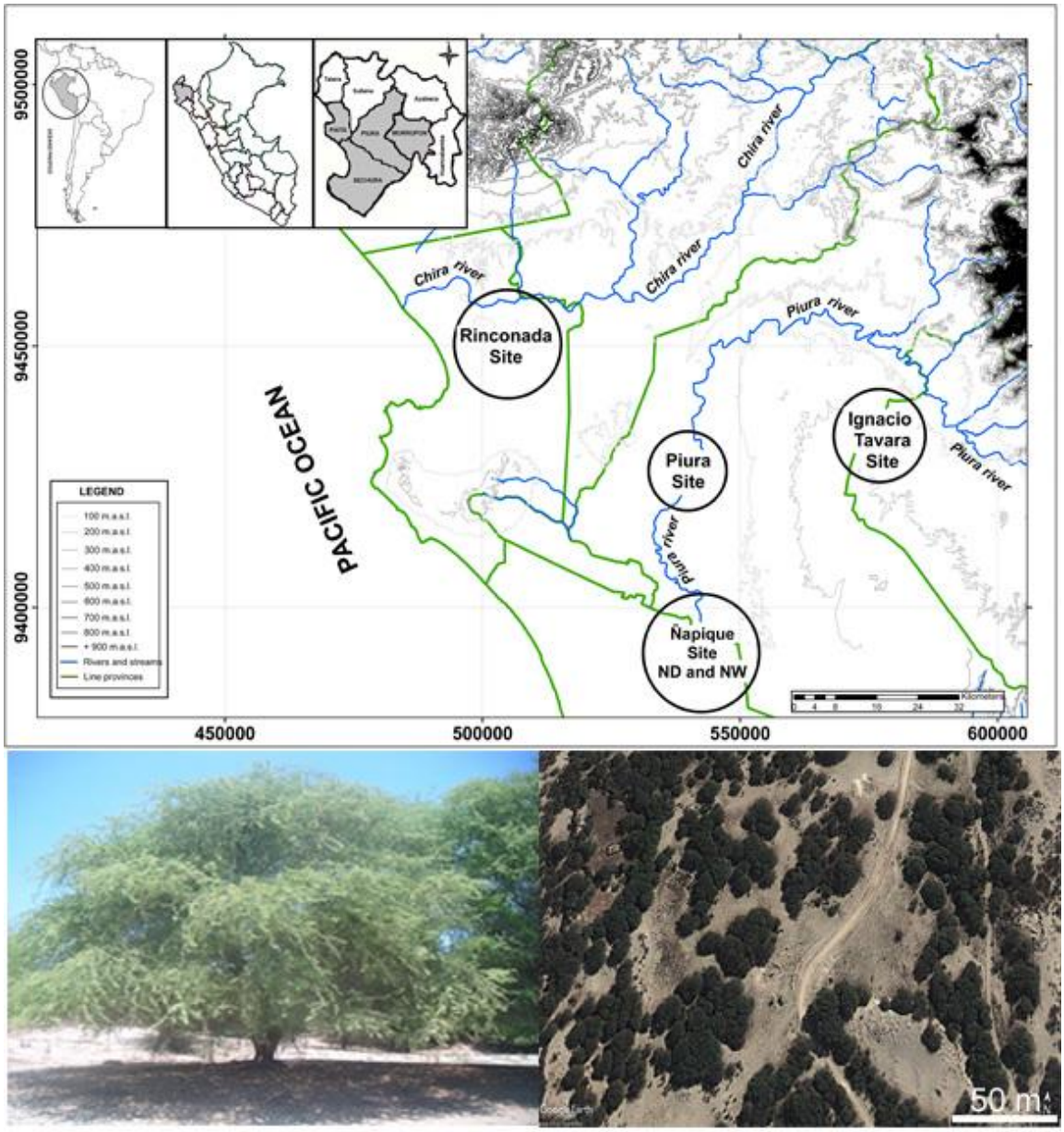

Figure 1. Locations of the five *Prosopis pallida* populations in Nort Peru dryland forests included in this study (top), tree and canopy structure of a sampled tree (bottom left), and landscape image of Ignacio Tavara site (bottom right).

Table 1. Climate description, soil features, plant traits, and location (UTM) of the studied zones. Data obtained from Climate Research Unit (CRU) as the mean values of the 2013, 2014 and 2015 summer periods. Zones were ordered according to mean annual precipitation. Mean ± SE values for pH and plant traits are shown. SPEI = Standardized precipitation-evapotranspiration index (low values indicate dry conditions).

	Ñapique Wet	**Ñapique Dry**	**Rinconada**	**Piura**	**Ignacio Tavara**
Zone Code	NW	ND	RI	PI	IT
Longitude	17 M 560606	17 M 560606	17 M 513373	17 M 532471	17 M 596277
Latitude	9405427	9405427	9457293	9433785	9434052
Mean summer precipitation (mm)	9.15 ± 2.1	9.15 ± 2.1	18.5 ± 2.7	37.8 ± 7	147 ± 20.3
Mean Summer temperature (ºC)	26.1 ± 0.2	26.1 ± 0.2	25.9 ± 0.2	26.6 ± 0.2	26.5 ± 0.1
SPEI	0.59 ± 0.81	0.59 ± 0.81	0.63 ± 0.25	0.13 ± 0.24	0.07 ± 0.26
Altitude (m a.s.l.)	15	15	97	73	153
Soil Texture	Sandy	Sandy	Sandy	Sandy	Sandy
Soil pH	6.85 ± 0.04	6.9 ± 0.04	6.51 ± 0.07	6.69 ± 0.04	6.45 ± 0.1
Tree Height (m)	8.24 ± 0.51	7.39 ± 0.43	11.12 ± 0.5	9.06 ± 0.74	8.77 ± 0.41
Tree Crown Area (m^2)	117.7 ± 12.8	80.5 ± 10.3	171.5 ± 24	68.5 ± 7.7	145.8 ± 19.4
DBH (m)	0.37 ± 0.05	0.24 ± 0.03	0.24 ± 0.03	0.15 ± 0.01	0.20 ± 0.02
LDMC (%)	28.06 ± 0.8	27.86 ± 0.6	24.43 ± 1	23.5 ± 0.9	33.27 ± 0.4
LMA (g m^{-2})	85.47 ± 3.4	87.94 ± 2.9	64.18 ± 4.1	66.11 ± 2.7	94.72 ± 3

Sampling design and data collection

Four *P. pallida* populations from the coast to foothills were selected to cover the climatic variability across the environmental gradient (Table 1). Due to one of them (Ñapique) presented high site variability related to the close proximity to a lake, this location was considered as two different populations (Ñapique Wet and Ñapique Dry, being the former the closest to the lake). Therefore, we considered a total of five populations. Their locations cover most of the North-Peruvian dryland forests, and plant cover was heavily dominated by *Prosopis pallida* trees. To cover the spatial and microclimatic variability within the site, two plots of 1 ha per population were established. The average distance between plots was 1265 m to avoid pseudo replication.

Within each plot, a random sampling inventory was developed and 4 adult trees of *P. pallida*, with a base stem diameter over 10 cm, were selected. Diameter at breast height (*DBH*, m) and height (*h*, m) were measured using a dendroflexometer (Herrera-Arreola et al., 2007; Ruiz et al., 2008). Tree crown area (m^2) was measured in two directions (N-S and E-W) and calculated using the eclipse equation. Individual tree locations were recorded with a real-time differential global positioning system (GPSMAP 76CSx - Garmin USA International, Inc; estimated position error <1 m). There was no plant species under the tree canopy of the selected trees. Each plot was compose mainly by *P. pallida* trees with random shrubs outside the canopy.

In each tree, 4 radiuses were established following cardinal axes. In March 2015, during no-ENSO conditions, four soil samples (10 cm diameter) were collected at 0–10 cm depths at a distance of 2, 4, 6, and 8 m from the tree base (Wang and Anderson, 1998). Surface unmineralized litter was not included in the sample (which varied between 0 and 5 cm in thickness). In all trees (n=40), the 8 m sample was located outside the canopy tree, except in 6 trees where the crown cover over 8 m. A subsample at 2 m from the tree was separated to measure pH and soil texture (see below). Samples from the same distance (four soil subsamples in each tree, from the four cardinal axes) were combined into a single sample. Soil samples were stored at 4 ºC in polyethylene bags until processing in the laboratory. All soil samples were air-dried at room temperature (25 °C), and were then sieved (mesh size 2 mm) to remove coarse living roots and gravel. Then, soil samples were oven dried at 70 °C for 24 h, and ground in a roller mill to a fine powder.

Soil and leaf analysis

Soil C, N, P, Cu, Fe, Mn and Zn concentrations were measured in all combined samples. Total organic C was determined using the LECO method, which combusts the organic carbon and measures the resulting carbon dioxide produced (Olsen et al., 1982). The soil available P was extracted with 0.5 M $NaHCO_3$ buffered at pH 8.5 for 30 min (Murphy and Riley, 1962) and measured colorimetrically (Norvell and Lindsay, 1972). Soil N was measured using an elemental analyzer (Eurovector EA 3000; EuroVector SpA, Milan, Italy). Soil extractable Mn, Cu, Fe and Zn were determined by atomic absorption spectrophotometry after extraction using Triethanolamine (TEA)

0.1 M, Diethylenetriaminepentaacetic acid (DTPA) 0.005 M and $CaCl_2$ 0.01 M (Sokal and Rohlf, 1995). Soil texture was measured in 50 g of soil sample using the Bouyoucos hydrometer Method. Soil pH was calculated in 20 g of soil sample using a portable pHmeter (GreenLine 8000) in 1:2.5 soil/water ratio.

In each tree, a fully expanded, sun-exposed branch was selected and mature leaves with no signs of damages were collected and transported in hermetic bags inside a portable cooler to measure leaf mass per area (LMA, g $m^{-}2$), leaf dry matter content (LDMC, %) and leaf nutrient concentration, Leaves (including petiole) were scanned and leaf area was calculated using Image-Pro plus v 4.5.0.29 software (Media Cybernetics, MD, USA). Leaf dry mass was measured after drying the leaf for 24 hours at 80 ºC and using an analytic balance. LMA was calculated as the ratio of leaf dry mass and area. A subsample of fresh leaves was selected from each tree in the field and taken in a portable cooler to calculate LDMC. In the laboratory, the leaves were taken to full water saturation and weighted 10 hours later. Finally, the leaves were dried during 24 hours at 80 ºC and weighed again. LDMC was calculated as the dry leaf mass divided by the full water-saturated leaf mass (Murphy and Riley, 1962). Finally, the material was ground and pass through a 0.5 mm screen for leaf nutrient composition. After a digestion with nitric/perchloric acid the resulting solution was analysed by atomic absorption spectrophotometry for Fe, Mn, Cu and Zn. P was analysed by the colorimetric method (Buschiazzo et al., 2001; Herrera-Arreola et al., 2007; Ruiz et al., 2008) and C and N following the same methodology applied for soil nutrient concentration.

Statistical analysis

We examined all variables to fit the assumptions of normality and homogeneity of variance, using the Kolmogorov–Smirnov and Levene test, respectively. When the data distribution did not fit in a normal distribution, the data were normalized by $\log_{10}$ transformations. Once the basic requirements were found to be met, a factorial analysis of variance (ANOVA) was used to determinate any statistical differences in soil nutrient concentrations at different distances from the tree (grouping factor 1, four levels) and between populations (grouping factor 2, five levels). When variables showed

significant differences, a Tukey test was used to detect differences between populations (R Development Core Team, 2013; Warton et al., 2013).

Then, we calculated a proximity index of soil samples to the tree base as the ratio of the distance of soil sample to the tree base and the tree crown radius. Therefore, when this variable is lower than 1, the soil sample comes from inside the tree canopy, and when is higher than 1, from outside the tree canopy. We made Pearson's correlation analyses between the proximity index and all soil measurements to study the spatial gradient of soil fertility around the tree.

To explore the relationship between tree size, leaf structural traits and leaf nutrient concentration with soil nutrient concentration, Pearson's correlation analyses were made.

We carried out a Standardized Major Axis (SMA) regression to study the differences between populations using factors that showed a significant correlation with the mean soil nutrient concentration. We compared the slopes of the linear regressions of each populations. Thus, populations with a more positive slope will have a higher fertility island effect.

Anova analyses and correlation analyses were made using STATISTICA v8.0 (StatSoft, Inc. 2007). SMA analyses were made using the package "smatr" of the software R (Kemp et al., 2003; Ordoñez et al., 2009).

Results

Effect of the distance to P. pallida tree on soil nutrient concentration

Soil nutrient concentration was not statistically different for any nutrient at 2, 4, 6 or 8 m distance from the tree (Table 2). Carbon, N and P soil concentration, were higher at 2 than 8 m from the tree, but no significant differences were found and the amount of variance explained was extremely low (about 1%, Table 3). Yet, we found a negative correlation between the proximity index and the soil C, N, Fe and Mn concentration (Fig. 2). Thus, soil nutrient concentration is slightly higher under the tree canopy, indicating the existence of a fertility island effect. The highest correlation was found in the soil Mn concentration (Fig. 2).

Table 2. Results of a two-way ANOVA for all soil nutrient concentration studied (n =160) with factors "distance from the tree base" (D) and "population" (P). The proportion of the explained variance (SS_x/SS_{total}) and the level of significance (*** $P < 0.001$) for each factor and the interactions are indicated. R^2 (×100) is the percentage of total variance absorbed by the model. Significant correlations are indicated in bold letter.

Nutrient concentration	Distance (D)	Population (P)	D×P	R^2
C (%)	0.01	**0.35*** **	0.01	**0.28*** **
N (%)	0.01	**0.46*** **	0.01	**0.40*** **
P (mg g^{-1})	0.01	**0.44*** **	0.01	**0.38*** **
Zn (mg kg^{-1})	0.01	**0.32*** **	0.02	**0.35*** **
Cu (mg kg^{-1})	0.01	**0.26*** **	0.02	**0.29*** **
Mn (mg kg^{-1})	0.01	**0.63*** **	0.01	**0.60*** **
Fe (mg kg^{-1})	0.00	**0.33*** **	0.01	**0.26*** **

Table 3. Soil nutrient concentration (mean ± SE) along different distances from the tree stem base (n =8) for the different populations. Different superscript letters indicate significant differences between Population at ($P \leq 0.05$) (Factorial ANOVA; Tukey test). See Table 1 for acronyms.

Population	Distance (m)	C (%)	N (%)	P (mg g^{-1})	Zn (mg kg^{-1})	Cu (mg kg^{-1})	Mn (mg kg^{-1})	Fe (mg kg^{-1})
NW	2	0.46±0.08	0.04±0.01	1.38±0.1	0.99±0.2	4.3±1.2	4.78±1.1	22.84±2.5
	4	0.45±0.05	0.04±0.01	1.14±0.1	0.75±0.1	2.9±0.8	4.04±0.5	21.89±2.3
	6	0.38±0.02	0.03±0.01	1.2±0.1	1.02±0.2	4.4±1.2	3.93±0.7	21.86±2.5
	8	0.36±0.02	0.03±0.01	1.23±0.1	1.21±0.3	4.2±1.5	3.85±0.7	22.24±3
Population average		0.41±0.02^{c}	0.04±0.01^{c}	1.23±0.1^{b}	1±0.1^{b}	4±0.6^{b}	4.15±0.4^{c}	22.21±1.2^{a}
ND	2	0.38±0.05	0.03±0.01	1.41±0.2	0.96±0.2	4.8±2.0	2.26±0.2	12.83±1.4
	4	0.32±0.05	0.02±0.01	1.18±0.1	0.76±0.3	3.1±1.9	2.02±0.3	13.86±2.1
	6	0.32±0.05	0.02±0.01	1.05±0.1	0.84±0.2	3.7±1.8	2.38±0.3	14.16±2
	8	0.28±0.04	0.02±0.01	1.05±0.2	0.56±0.2	2.3±1.6	2.01±0.3	11.73±2
Population average		0.32±0.02^{c}	0.02±0.01^{c}	1.17±0.1^{b}	0.79±0.1^{b}	3.5±0.9^{b}	2.17±0.1^{c}	13.14±1^{b}
RI	2	1.49±0.47	0.19±0.06	2.87±0.6	2.45±0.4	14.5±3.3	14.55±2.9	23.18±4.5
	4	1.07±0.25	0.15±0.03	2.71±0.5	1.93±0.3	11.9±3.3	12.16±2.5	19.9±3.7
	6	1.24±0.28	0.16±0.03	2.93±0.5	2.16±0.4	17.2±3.7	13.23±2.7	23.41±4.4
	8	1.22±0.28	0.16±0.03	3.02±0.5	2.24±0.3	14.1±2.7	13.02±2.1	20.94±3.3
Population average		1.25±0.16^{a}	0.16±0.02^{a}	2.88±0.2^{a}	2.19±0.2^{a}	14.4±1.6^{a}	13.23±1.2^{a}	21.85±1.9^{a}
PI	2	0.45±0.07	0.05±0.01	1.2±0.2	2.29±0.4	13.4±1.4	7.48±0.8	15.55±1.2
	4	0.45±0.06	0.05±0.01	1.14±0.1	2.07±0.4	14.5±1.8	6.51±0.5	15.31±1.1
	6	0.41±0.04	0.05±0.01	1.1±0.1	2.04±0.3	12.6±1.2	6.64±0.4	14.93±1.1
	8	0.39±0.04	0.05±0.01	1.16±0.1	2.02±0.4	12.6±1.4	6.42±0.2	16.15±1.1
Population average		0.42±0.3^{c}	0.05±0.01^{bc}	1.15±0.1^{b}	2.1±0.2^{a}	13.3±0.7^{a}	6.76±0.3^{b}	15.49±0.5^{b}
IT	2	0.84±0.04	0.09±0.01	1.45±0.1	1.96±0.2	11.2±3.6	14.01±0.7	24.55±2.3
	4	0.77±0.07	0.08±0.01	1.28±0.1	1.67±0.2	9.4±3.5	13.26±1.0	22.45±1.2
	6	0.66±0.1	0.07±0.01	1.26±0.1	1.62±0.2	8.8±3.4	12.64±0.7	21.38±1.4
	8	0.68±0.07	0.07±0.01	1.18±0.1	1.99±0.3	10±4.2	10.58±1.1	23.62±2.4
Population average		0.74±0.03^{b}	0.07±0.01^{b}	1.29±0.1^{b}	1.81±0.1^{a}	9.9±1.7^{a}	12.62±0.5^{a}	23±0.9^{a}

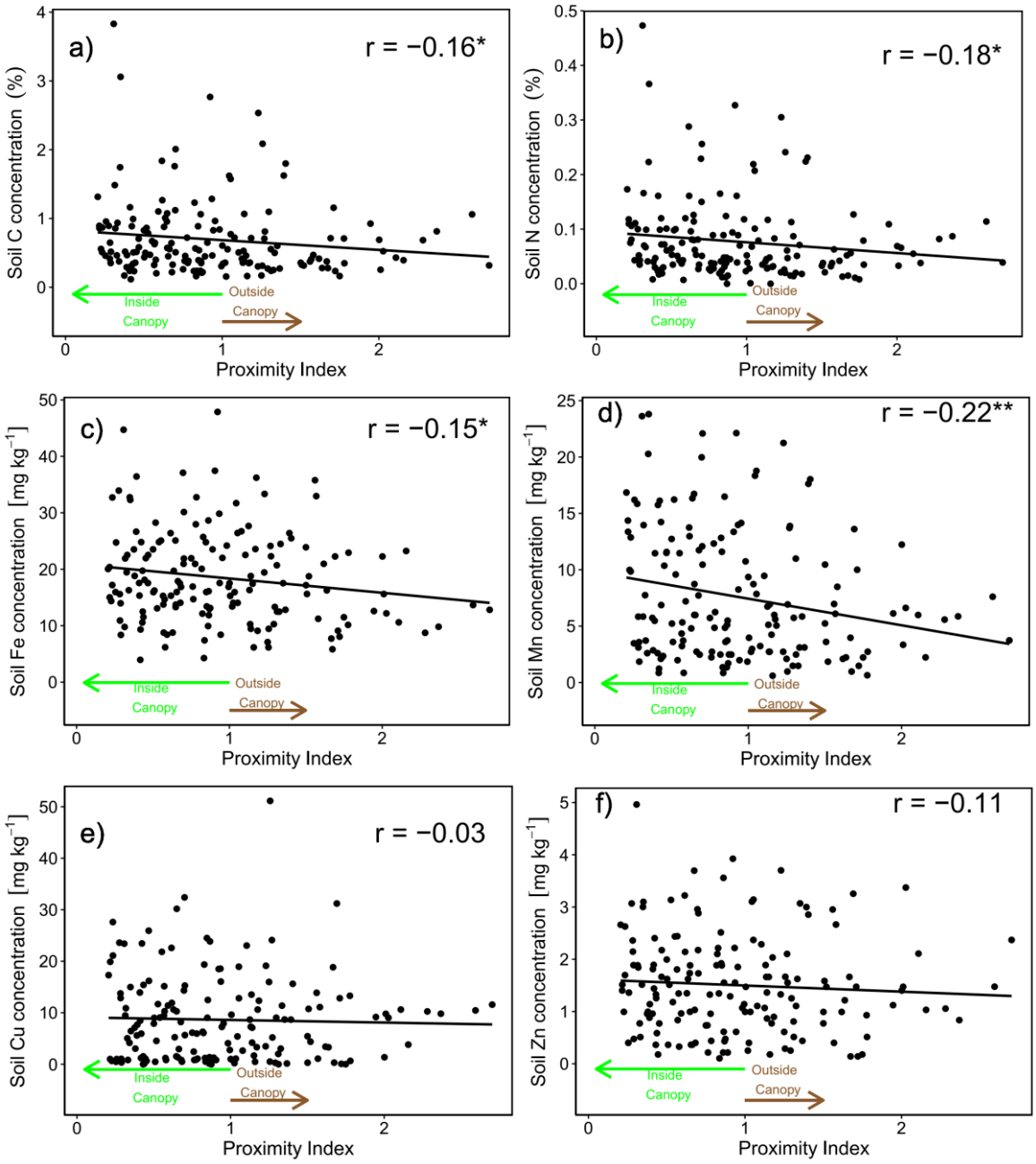

Figure 2. Relationships between soil nutrient concentration and the proximity index from the tree base to the canopy interspace **a**) C, **b**) N, **c**) Fe, **d**) Mn, **e**) Cu and **f**) Zn. Significant correlation are shown (* P <0.05).

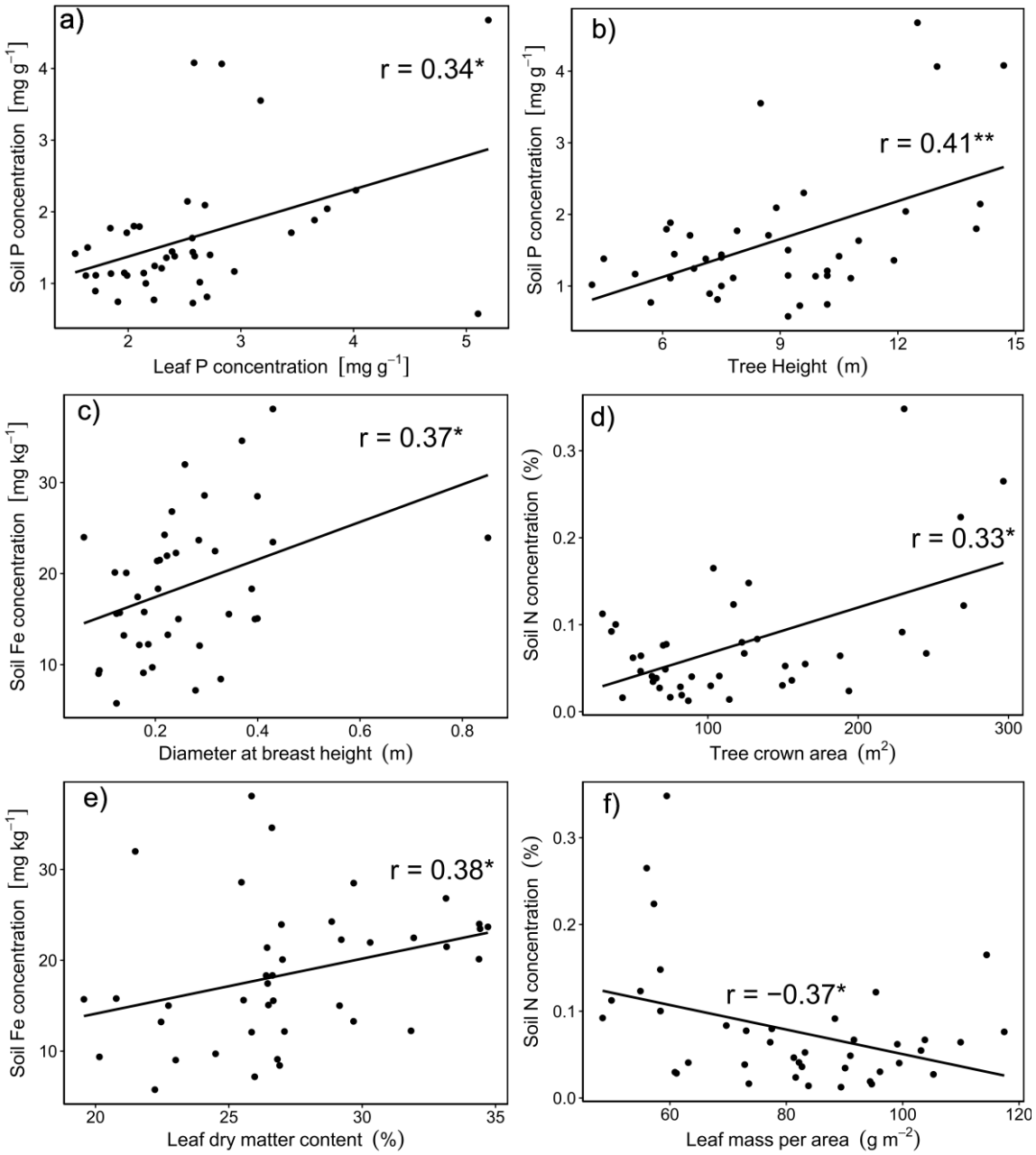

Figure 3. Relationships between the mean soil nutrient concentration and **a**) leaf P concentration, **b**) tree height, **c**) diameter at breast height, **d**) tree crown area, **e**) LDMC, and **f**) LMA. Significant correlation are shown (* P <0.05, ** P <0.01, and *** P <0.001).

Influences of plant size and leaf traits on soil nutrient concentration

Leaf P and N concentration were positively correlated to soil P and N concentration at 8 m respectively (Table 4 and Fig. 3). For the other nutrients, there was no significant relationship between leaf and soil nutrient concentration except for Mn concentration at 2, 4 and 6 m distance (Table 4).

Finally, mean soil P concentration was positively correlated to leaf P concentration (Table 4).

Table 4. Pearson correlation coefficients between leaf nutrient, soil nutrient at different distances from the tree, and the mean value from all distances. Significant correlations are indicated in bold letter (* P <0.05)

Nutrient concentration	Distance from the tree				
	2 m	4 m	6 m	8 m	Soil mean Concentration
C (%)	-0.21	-0.20	-0.25	-0.18	-0.24
N (%)	0.25	0.23	0.24	**0.39***	0.23
P (mg g^{-1})	0.21	0.27	0.21	**0.40***	**0.34***
Zn (mg kg^{-1})	0.27	0.23	0.06	0.11	0.10
Cu (mg kg^{-1})	-0.05	-0.16	-0.09	-0.07	-0.06
Mn (mg kg^{-1})	**0.37***	**0.37***	**0.35***	0.25	0.30
Fe (mg kg^{-1})	0.17	0.17	0.22	0.22	0.21

Tree size was positively correlated with soil nutrient concentration. Tree height was positively correlated to mean soil C, N, P concentration, and soil Mn concentration at 8m from tree (Table 5 and Fig. 3). Tree crown area was correlated also to C, N, Mn and Fe soil concentration, while diameter at breast height was correlated to mean soil Fe concentration (Table 5) and at all distances. While mean soil N concentration was correlated with Tree crown area. Similarly, some leaf traits showed significant correlations with soil nutrient concentration (Table 6). Mean soil N, P and C concentration was negatively correlated with leaf mass per area (and at 6 and 8 m from the tree). Also mean soil Fe concentration (and at 2, 4 and 8 m) was positively correlated with leaf dry matter content (Table 6).

Table 5. Pearson correlation coefficients between tree size, soil nutrient concentration at different distances from the tree, and the mean value from all distances. Significant correlations are indicated in bold letter (* P <0.05, ** P <0.01, and *** P <0.001).

Soil nutrients	Tree size	Distance from the tree				
		2m	4m	6m	8m	Soil mean concentration
C (%)	Tree Height (m)	**0.45****	**0.55*****	**0.47****	**0.52*****	**0.54*****
N (%)		**0.47****	**0.56*****	**0.44****	**0.54*****	**0.58*****
P (mg g^{-1})		0.25	0.31	**0.37***	**0.36***	**0.41****
Zn (mg kg^{-1})		-0.04	0.13	0.06	0.24	0.17
Cu (mg kg^{-1})		0.12	0.13	0.09	0.21	0.19
Mn (mg kg^{-1})		0.2	0.3	0.19	**0.33***	0.30
Fe (mg kg^{-1})		0.09	0.11	0.1	0.16	0.16
C (%)	Diameter at breast height (m)	0.01	0.02	-0.07	-0.06	-0.06
N (%)		-0.04	-0.05	-0.16	-0.1	-0.12
P (mg g^{-1})		0.13	0.02	-0.07	-0.09	-0.02
Zn (mg kg^{-1})		0.03	-0.07	-0.08	-0.05	-0.06
Cu (mg kg^{-1})		-0.1	-0.18	-0.24	-0.21	-0.20
Mn (mg kg^{-1})		-0.06	-0.06	0.04	-0.17	-0.14
Fe (mg kg^{-1})		**0.43***	**0.45****	**0.38***	**0.38***	**0.37***
C (%)	Tree crown area (m^2)	**0.3**	**0.33***	0.2	**0.35***	0.30
N (%)		**0.35***	**0.35***	0.12	**0.34***	**0.33***
P (mg g^{-1})		0.17	0.17	0.11	0.11	0.18
Zn (mg kg^{-1})		0.29	0.23	0.11	0.28	0.26
Cu (mg kg^{-1})		-0.01	-0.05	-0.16	-0.05	-0.05
Mn (mg kg^{-1})		**0.37***	**0.46****	**0.49****	**0.42****	**0.40***
Fe (mg kg^{-1})		**0.48****	**0.50****	**0.46****	**0.51****	**0.50****

Differences of fertility island effect between populations

Soil nutrient concentration was significantly different among populations. Tukey test showed that soil nutrient concentration was significantly higher in Rinconada (RI) than in the other populations (Table 2). While, Ñapique Dry and Ñapique Wet showed the lowest soil nutrient concentration. Manganese concentration differences showed the highest proportion of variance (around 60 %) explained by the population (Table 3).

Table 6. Pearson correlation coefficients between leaf structural traits, soil nutrient concentration at different distances from the tree, and the mean value from all distances. Significant correlations are indicated in bold letter (* P <0.05).

Soil nutrients	Leaf trait	Distance from the tree				
		2m	4m	6m	8m	Soil mean concentration
C (%)	Leaf dry matter content (%)	-0.02	0.01	-0.12	-0.12	-0.05
N (%)		-0.05	-0.06	-0.17	-0.18	-0.10
P (mg kg^{-1})		-0.12	-0.14	-0.25	**-0.41***	-0.27
Zn (mg kg^{-1})		-0.02	0.02	0.05	0.07	0.05
Cu (mg kg^{-1})		-0.02	-0.01	-0.09	-0.06	-0.08
Mn (mg kg^{-1})		0.22	0.24	0.32	0.10	0.23
Fe (mg kg^{-1})		**0.38***	**0.39***	**0.34***	**0.37***	**0.38***
C (%)	Leaf mass per area (g m^{-2})	-0.26	-0.23	-0.30	**-0.37***	**-0.31***
N (%)		-0.31	-0.30	**-0.31**	**-0.43****	**-0.37***
P (mg kg^{-1})		-0.23	-0.28	**-0.35***	**-0.38***	**-0.37***
Zn (mg kg^{-1})		-0.13	-0.07	-0.04	-0.08	-0.10
Cu (mg kg^{-1})		-0.18	-0.14	-0.20	-0.24	-0.24
Mn (mg kg^{-1})		0.02	0.05	0.14	-0.12	-0.01
Fe (mg kg^{-1})		0.29	0.31	0.22	0.16	0.24

Table 7. Standardized Major Axis (SMA) regressions of soil nutrient concentration and tree size, leaf structural traits and leaf nutrient composition. The value of the regression slope (the scaling exponent from major axis regression) for the total regional pool and for each different studied populations is shown (n = 8). Significance level (*P < 0.05, **P < 0.01, ***P<0.001) is also shown.

Log_{10} X	Log_{10} Y	Total Pool (n = 40)	Population				
			NW	ND	RI	PI	IT
Tree Height (m)	Soil [C]	**1.94*****	0.84	0.99	**3.40***	**1.05***	-0.99
	Soil [N]	**2.62*****	1.11	1.59	**3.17***	**0.95***	1.00
	Soil [P]	**1.40****	1.05	-1.28	2.22	**0.66***	-0.74
Tree Crown Area (m^2)	Soil [N]	**1..37***	0.64	1.00	**1.33***	-0.82	0.38
	Soil [Mn]	**1.37***	-1.2	0.98	0.84	-0.41	-0.22
	Soil [Fe]	**0.69****	-0.79	0.91	**0.80***	-0.46	0.13
DBH (m)	Soil [Fe]	**0.90***	0.62	-1.35	**1.21***	0.68	0.16
Leaf [P]	Soil [P]	**1.53***	1.21	2.44	-2.32	2.02	1.16
LMA (g m^{-2})	Soil [C]	**-2.43***	-1.18	2.78	-5.46	-2.39	2.29
	Soil [N]	**-3.27***	-1.67	4.41	-5.10	-2.18	-2.41
	Soil [P]	**-1.73***	-1.47	4.04	-3.55	-1.46	1.79
LDMC (%)	Soil [Fe]	**2.88***	5.78	6.46	3.77	-1.73	2.03

The SMA analysis considering only the most significant traits correlated to soil nutrients concentrations showed that linear regressions slopes were higher in Rinconada (RI) than the regional pool slopes (Table 7). Thus, the effect of tree height over soil C and N concentration was higher in RI than in other populations (Fig 4a and b). Similarly, the effect of diameter at breast height and tree crown area over soil Fe concentration was also higher in RI than in other populations. In other population (Piura, PI), the trees showed a small effect on soil nutrient, as the effect of tree height on soil C and N concentration was lower in PI than in any other population (Table 7).

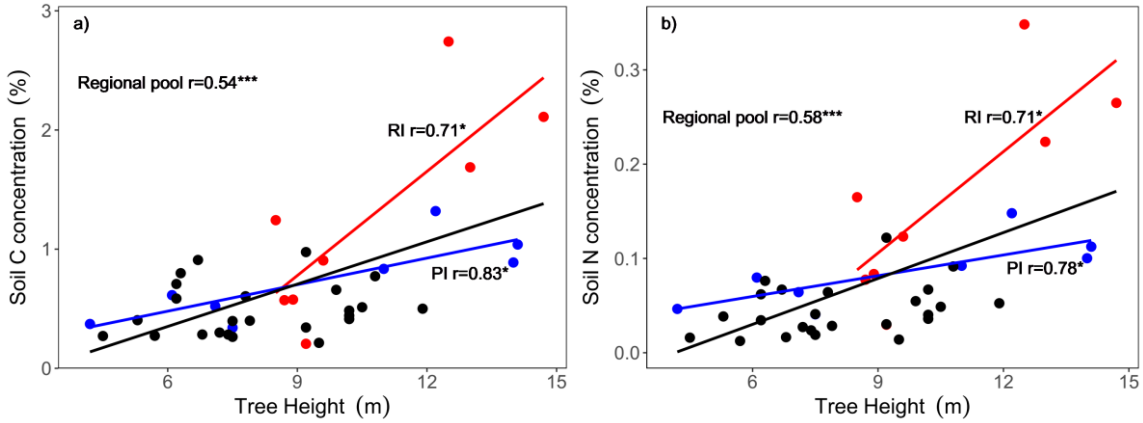

Figure 4. Relationships between tree height and a) soil C, and b) soil N concentration. Correlation coefficient and significance level is shown (*$P < 0.05$, ***$P < 0.001$).

Discussion

Our results indicate that the soil nutrient concentration is higher under *Prosopis pallida* tree canopy. Additionally, tree size, leaf structure and nutrient composition played a major role on the fertility island effect in the dryland forest of North Peru. And this effect can be different between populations due to local climatic conditions

Fertility island effect of Prosopis pallida

The high *Prosopis pallida* coverage in the Northern Peruvian dryland forest suggest this species should play an important role in soil nutrient concentration variability, similar to what has been found in other related species (*P. caldenia*, *P. laevigata* and *P. juliflora*) where organic material, microbial biomass, and C concentration were higher near the tree (Buschiazzo et al., 2001; Curiel Yuste et al., 2003). However, the small effect of *P. pallida* on soil nutrient spatial distribution contrast with these previous results.

Several factors could have contributed to the reduction of the spatial effect of the fertility island. Primary, low precipitation in this region during the no-ENSO season reduces leaf litter biomass production and diminishes the amount of organic input from the tree into the soil. This also slow down leaf litter decomposition (Abril et al., 2009; White et al., 2009), soil microbial activity (Rollenbeck et al., 2015), and therefore the overall fertility island effect.

Aeolian transport processes could have also weakened the fertility island effect. Soil structure and nutrient input are highly influenced by wind dynamics in arid ecosystems (Austin et al., 2004). The climate in the North Peruvian dryland forest is influenced by a strong wind field stream with a wind speed up to 25km h^{-1} to north due to the Humboldt current (Fraisse et al., 2010), similar to those found in Paracas (Briceño-Zuluaga et al., 2017), which spread the leaf litter in and out of *Prosopis* canopy and partially reducing the spatial effect of the fertility island.

Soil nutrient concentration also depends on other soil features like texture. For example, the lack of clay or silt would enhance nutrient leaching, reducing the effect of the fertility island during rainy events (Herrera-Arreola et al., 2007). Thus, strong rainfall events like the ENSO phenomenon could have lixiviated soil nutrients below the tree canopy, reducing soil fertility (Qi et al., 2010). However, nutrient redistribution by capillary rise should increase nutrient content in the soil surface after such event. Thus, more data is required to determinate how extreme flooding events and soil texture affect vertical soil nutrient distribution.

Influences of plant size and leaf traits on soil nutrient concentration

Besides the effect of tree proximity on soil nutrient distribution, tree size, leaf structure, and leaf nutrient concentration significantly correlate with soil nutrients. The highest significance was found in most cases at 8 m distance from the tree. Probably because soil microorganism, root respiration, and organic input from small mammals alter the fertility island effect too close to the tree base (Schade et al., 2003). The significant relationships between tree height, tree crown area, and leaf nutrient concentration on soil C, N and P concentration indicate that fertility island effect of *Prosopis pallida* represent a quantitative and qualitative increase in leaf litter content, which is the main

source of soil nutrients (Ruiz et al., 2008). Moreover, tree canopy provides better conditions to soil microorganism activity reducing temperature and evapotranspiration (Fan et al., 2015; Lü et al., 2012). Thus, without plant cover, the microclimatic variation in the soil reduces soil humidity and microbial activity (Jarrell and Virginia, 1990).

The significant relationship between tree size and trace elements can be explained by the tight relationship in soil nutrient absorption. For instance, the positive effect of tree size and soil Fe can be explained because nitrate and Fe absorption occurs simultaneously in the roots of *Prosopis glandulosa* (Ordoñez et al., 2009). Similarly, leaf and soil Mn concentration showed a significant positive correlation, and suggest this element is constantly exchanged between tree and soil. Mn is an essential nutrient for biochemical processes inside the leaf as the activator of several enzymes and it is quite sensitive to soil pH (White et al., 2009). Under unfertile soils, roots exudates can reduce soil pH to increase nutrient availability of scarce elements like P and N (Lambers et al., 2015), and increase Mn uptake along with it. Thus, it has been suggested that leaf Mn can be used to track soil nutrient acquisition strategies (Villegas et al., 2010). In *Prosopis velutina* a significant decrease in soil pH under the tree has been found (Bates et al., 2008), suggesting it has been the result of root exudates. Therefore pH modulation to increase nutrient availability in this species is possible, and it could explain the accumulation of soil Mn from leaf litter under the tree canopy. The relationship between soil and leaf nutrient concentration found in our study strengthen the importance of *P. pallida* for soil fertility. Therefore, tree size and leaf nutrient concentration plays an important role in soil fertility under extremely arid conditions.

Leaf structural traits (LMA and LDMC) are also related to soil nutrient concentration. Leaf mass per area is a good indicator of leaf carbon investment and is related to plant physiology and drought resistance (Allison and Vitousek, 2004). Low LMA is common in plants with an acquisitive strategy, with high photosynthetic rates per unit mass and leaf nitrogen concentration. In *Propopis pallida* we have found a negative correlation between LMA and leaf N concentration (Capítulo 4). This could explain the negative correlation of LMA with soil N concentration. Leaf N and P concentration were also correlated to soil N and P concentration, respectively.

This suggests that leaf structure in *P. pallida* also influence litter quality, and it explain the relationships between functional traits and soil nutrient concentration (Gallaher and Merlin, 2010). Similar relationships have been found before in *P. pallida* (Burnell, 1988), and it may be related to the increased plant colonization below tree canopies (Bashan et al., 2000). Thus, our results indicate that leaf functional traits and leaf nutrient composition, alongside tree size, are mostly responsible for the fertility island effect.

Differences of fertility island effect between populations

Soil nutrient concentration was significantly different among *P. pallida* populations, Rinconada showed the highest soil nutrient concentration in all cases. Also, the relationship between soil C and N and tree height showed a steeper slope in RI than in the regional pool. Similarly, the relationship between tree crown, DBH and soil Fe showed a steeper slope in RI. This may indicate that the effect of tree size on the fertility island effect is stronger in this population than in any other. These results could be related to the proximity of RI to the sea (Fig. 1), where sea breeze reduces summer temperature and evapotranspiration. This, alongside low pH, could provide beneficial microclimatic conditions that boost nutrient uptake, biomass production and soil microbial activity in this population.

High tree height, tree diameter and tree canopy in RI produce more leaf litter biomass under this better/more favorable climatic conditions. An increase of litter quality (low LMA and high leaf N concentration) in RI should also enhance microbial activity and the overall soil nutrient concentration (Olsen et al., 1982). Thus, this result indicate that the combined effect of plant traits, climatic conditions and acid soil pH could increase fertility island effect, and it suggest that the ecological benefits of *Prosopis pallida* on soil nutrient concentration can be increased under these conditions. Oppositely, with the rise of mean temperature and rainfall reduction in many dryland ecosystems due to global warming (Beguería et al., 2014), fertility islands in *Prosopis* forests in North America and Africa should expected a drawback in nutrient recycling.

Conclusions

Utterly, our results showed that the fertility island effect in *P. pallida* populations in North Peru increase soil C, N, P, Fe and Mn despite the limited rainfall conditions and high temperatures during the no-ENSO season. This effect depends on tree size, leaf structural traits and leaf nutrient concentration, which increase leaf litter quantitatively and qualitatively. The fertility island effect was stronger in coastal populations, where climatic and edaphic conditions creates favorable microclimatic conditions for biomass production and nutrient decomposition Forest conservation programs could include this species as nursery plant in reforestation processes to increase soil nutrient fertility.

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Capítulo 7

Discusión general

El objetivo general de esta tesis es conocer la variabilidad intraespecífica de un conjunto de poblaciones de *Prosopis pallida* (algarrobo) de la región de Piura, representativas del gradiente ecológico de la región, y su respuesta a la variabilidad espacio-temporal del clima y de las características del suelo. Para ello se han realizado medidas en poblaciones de algarrobo a lo largo de un gradiente climático, así como experimentos en condiciones controladas (invernadero). Los resultados obtenidos indican que el algarrobo responde a la variabilidad espacial y temporal de la temperatura y de la precipitación asociada al fenómeno de El Niño (ENSO, del inglés El Niño Southern Oscillation). Durante la fase húmeda del ENSO, el algarrobo es capaz de incrementar más de 4 veces su crecimiento radial, mientras que en la fase seca, la temperatura es el factor principal que está relacionado con la variabilidad funcional. Por otro lado, las características del suelo como el pH y la conductividad eléctrica condicionan significativamente la disponibilidad de los nutrientes del suelo hacia la planta, mientras que la calidad de la hoja y el tamaño del árbol afectan al retorno de nutrientes al suelo y al efecto de la isla de fertilidad.

Variabilidad espacio-temporal del crecimiento

Los resultados dendrocronológicos (***Capítulo 2***) demostraron que el crecimiento del algarrobo puede ser hasta 4 veces mayor durante el ENSO (fase húmeda) que en años normales (fase seca) (Fig. 1). El algarrobo es una especie reconocida tanto por su sensibilidad frente a los eventos climáticos extremos (López et al., 2005), como a condiciones de estrés, como la salinidad y la sequía (de Villalobos et al., 2002; Velarde et al., 2003), lo cual demuestra la alta plasticidad que presenta esta especie frente a los cambios de la disponibilidad hídrica a través del tiempo (Fig. 1).

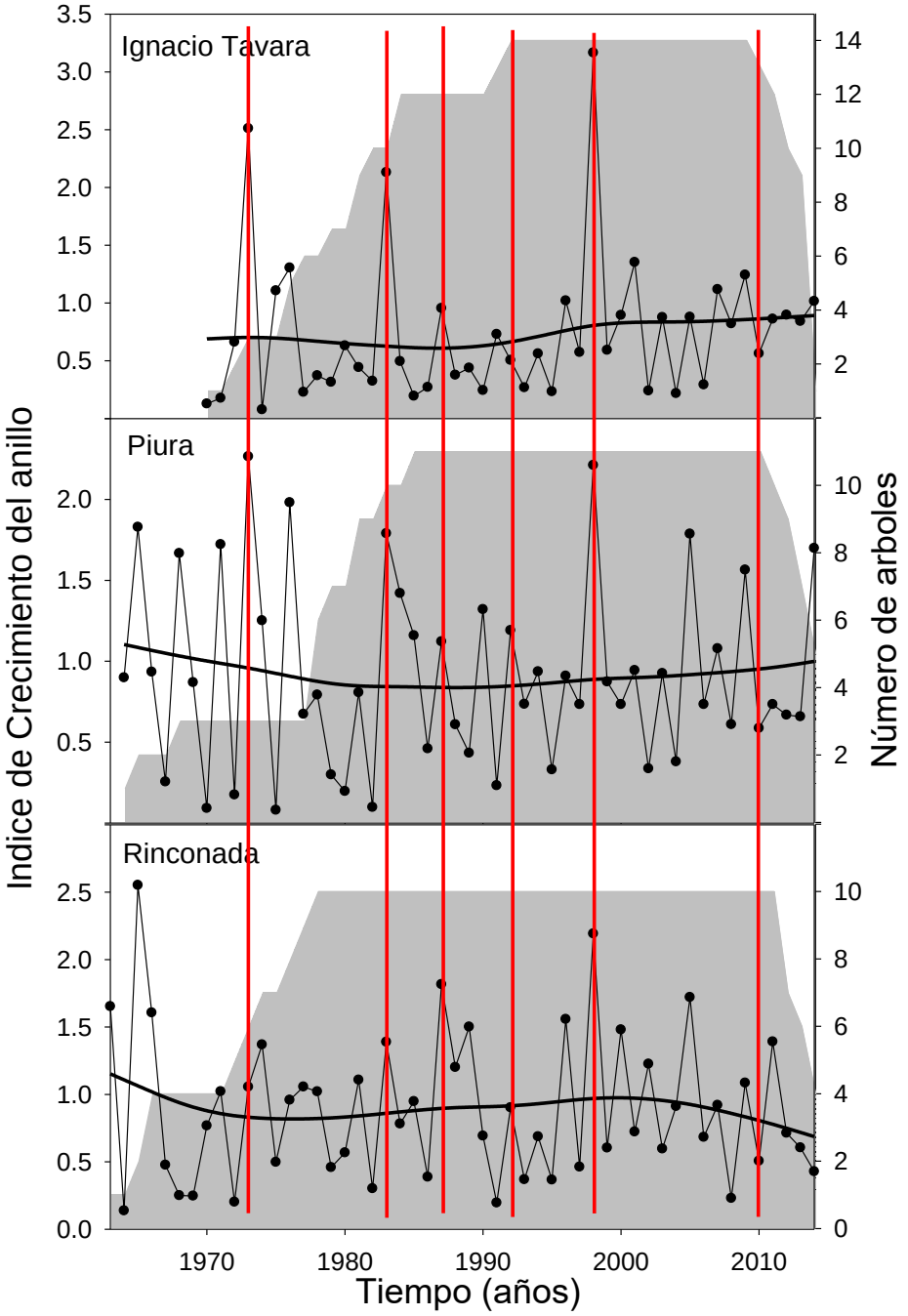

Figura 1. Índice de crecimiento de los anillos a lo largo del tiempo en 3 de las zonas de estudio de la región de Piura localizadas en un gradiente climático. Las líneas rojas indican los años donde ha ocurrido un Fenómeno El Niño (según las declaraciones de la NOOA, National Oceanic and Atmospheric Administration, EEUU). El área sombreada gris indica el número de árboles promediados en cada año para construir el índice de crecimiento.

El crecimiento radial del tronco responde positivamente a la precipitación y temperatura de verano (diciembre a marzo), que representa el periodo de mayor precipitación durante el ENSO. El incremento gradual de la temperatura del mar en el Océano Pacífico central (región 3.4) y el debilitamiento de la corriente de Humboldt, trae consigo un aumento en la temperatura en la costa norte de Perú (región Niño 1+2). La variabilidad de la temperatura en el Océano Pacífico ha dado lugar a la creación de indicies de temperatura oceánica para monitorear el comportamiento del ENSO. Encontramos fuerte correlación entre el crecimiento radial y el índice Niño 1+2 de la temperatura del mar. Esto se debe a la fuerte inercia térmica del Océano Pacífico, la cual liga la temperatura de la atmósfera con la del mar y, debido a la naturaleza tropical del territorio, con las precipitaciones en la costa de Sudamérica (Cai et al., 2015). El ENSO es un fenómeno global que afecta también a las condiciones ambientales en Asia, Norte América y África (Cai et al., 2015; de Ridder et al., 2013; Routson et al., 2016). Aunque el índice Nino 3.4 haya demostrado ser el indicador más eficiente para detectar y predecir la actividad del ENSO (Takahashi y Martínez, 2017), nuestros resultados sugieren que el crecimiento del algarrobo en la región de Piura depende de factores ambientales locales, lo cuales están regidos por indicadores de temperatura del mar costeros como el Niño 1+2 (Fig. 2).

Los resultados del experimento de invernadero (***Capítulo 3***) también indican un aumento de la biomasa total y la evapotranspiración en respuesta al incremento en la disponibilidad hídrica, favoreciendo el crecimiento (Fig. 2). El incremento de la biomasa se relacionó negativamente con el peso específico foliar (LMA), una variable reconocida por su relación negativa con el intercambio gaseoso y el consumo de recursos en la hoja (Wright et al., 2004). Además, el incremento de la biomasa también se relacionó positivamente con la distribución de biomasa de la raíz (RMR), lo cual podría favorecer el consumo de agua y el establecimiento de la planta (Vilela et al., 2003). El desarrollo de raíces profundas (que alcanzan la capa freática) y laterales en algarrobo son mecanismos comunes para aumentar la absorción de agua subterránea y agua de lluvia (Pasiecznik et al., 2001). Por tanto, nuestros resultados sugieren que un cambio en la estructura de la hoja, y un incremento en la absorción de agua permiten modular el crecimiento frente a eventos de alta precipitación como el ENSO.

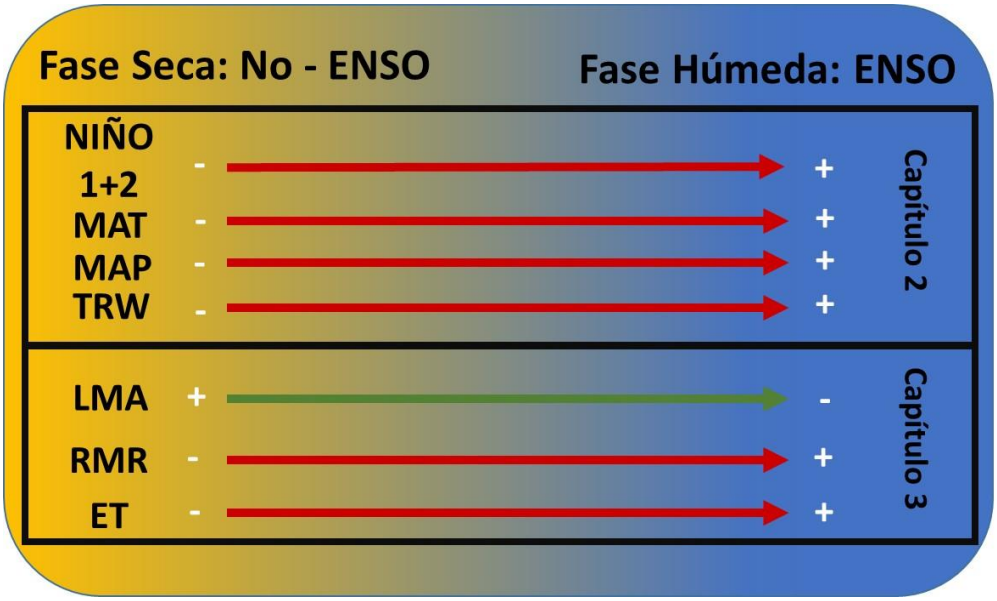

Figura 2. El ENSO, relacionado con el indicador Niño 1+2, aumenta la temperatura del aire y la precipitación media anual. Esto genera una respuesta fisiológica del algarrobo frente a la variabilidad climática, aumentando la evapotranspiración, el desarrollo de la raíz, el crecimiento, y disminuyendo el peso específico foliar. LMA: Peso específico foliar, MAP: Precipitación media anual, MAT: Temperatura media anual, RMR: porcentaje de raíz, TRW: índice de grosor de anillo.

Además de la respuesta del algarrobo frente a la variabilidad temporal de la disponibilidad hídrica, nuestros resultados indican que las poblaciones responden de manera diferente según las condiciones locales a lo largo del gradiente climático (***Capítulo 2***). A partir de los resultados dendrocronológicos se observa que la plasticidad del algarrobo frente a la disponibilidad hídrica es menor en poblaciones costeras (Rinconada) que en poblaciones continentales (Ignacio Távara) (Fig. 1). Se observa que el tamaño de los anillos de crecimiento durante el ENSO es menor en los árboles de la Rinconada que los de Ignacio Távara. Además, el coeficiente de correlación entre el crecimiento y la precipitación de verano es mayor en Ignacio Távara, y disminuye hacia la costa hasta no ser significativo (Rinconada). Esto se puede deber a una mayor intensidad de la precipitación en zonas continentales (Anexo 2) debido al efecto de la corriente de Walker que desplaza las nubes hacia el interior del continente (Erdmann et al., 2008). Por otra parte, la capa freática en estas zonas del interior del continente es de mayor profundidad, lo cual eleva su dependencia climática (Giantomasi et al., 2013). A pesar de ello, los resultados del experimento de

invernadero indican que la plasticidad de las poblaciones de algarrobo frente a la disponibilidad hídrica no está relacionada con la precipitación o con su variación temporal local. Por tanto, aunque la plasticidad poblacional del algarrobo permite maximizar el desarrollo según las condiciones locales, esta plasticidad no parece ser un factor heredable (Schneider y Meyer, 2017).

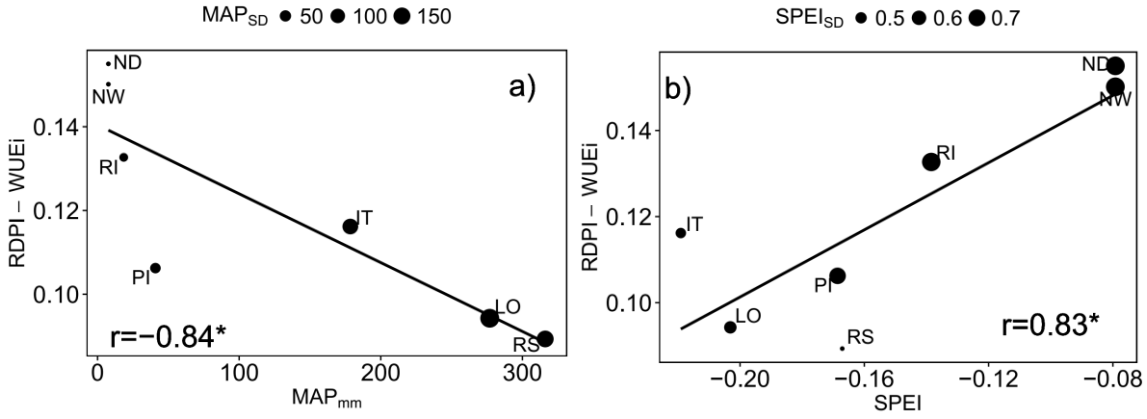

Figura 3. Relaciones entre la plasticidad (RDPI- Relative Distance Plasticity Index, Valladares et al, 2006) de la eficiencia instantánea en el uso del agua del algarrobo y la precipitación media anual (**a**) y el índice estandarizado de precipitación-evapotranspiración (SPEI) (**b**) en cada población. El tamaño de los puntos indica la desviación estándar de cada localidad.

La eficiencia instantánea en el uso del agua (WUEi) fue la única variable del experimento de invernadero (***Capítulo 3***) cuya plasticidad presentó una correlación significativa con la precipitación y con un índice de sequía (índice SPEI- Standardized Precipitation Evapotranspiration Index) del lugar de procedencia (Fig. 3). Los valores más bajos de el índice SPEI indican un mayor estrés por sequía (Beguería et al., 2014). La correlación positiva entre el WUEi y el SPEI (Fig. 3b) sugiere que la plasticidad está limitada por las condiciones limitantes o de estrés, y que el intercambio gaseoso puede ser una característica dependiente de las condiciones externas. Las zonas con mayor evapotranspiración son también las poblaciones con mayor precipitación y mayor variabilidad de la misma, esto es debido a que un aumento de la precipitación está asociado a un aumento de la temperatura, lo cual incrementa la evapotranspiración y determina valores más bajos de SPEI. Estos resultados sugieren que las condiciones de estrés van a inducir poblaciones menos plásticas. Sin embargo, aún es necesario realizar más estudios para determinar

hasta qué punto la plasticidad del intercambio gaseoso puede ser un rasgo heredable.

La fase seca del ENSO representa un periodo de alta estabilidad climática, donde las precipitaciones no superan los 300 mm anuales en las zonas más lluviosas. En cambio, otras variables como la temperatura, la humedad relativa y la radiación siguen ciclos anuales estables y predecibles. Debido a la baja precipitación y a la alta radiación y temperatura, esta fase representa un largo periodo de sequía (5 a 10 años) donde el crecimiento y la reproducción de las plantas estarán restringidos, y la resistencia al estrés será un factor adaptativo crucial para la supervivencia (Holmgren et al., 2001).

La plasticidad de algunas variables sí parece estar relacionada con los factores ambientales. Además del WUEi (que se discutió previamente), se ha encontrado una correlación negativa entre la plasticidad de la altura de la planta y la temperatura media anual. Lo cual sugiere que altas temperaturas sí podrían tener un papel restrictivo sobre la diversidad genética, limitando la plasticidad. De manera similar, nuestros resultados de campo muestran que la temperatura media anual se correlacionó con las variables asociadas a la regulación hídrica de la hoja (***Capítulo 4***). En *Prosopis tamarugo* y *P. chilensis*, un incremento de la temperatura tiene un efecto negativo sobre la tasa fotosintética (Delatorre et al., 2008), y lo mismo ocurre en *Prosopis juliflora*, donde el valor de WUEi incrementa al subir la temperatura (Elfadl y Luukkanen, 2006). Por tanto, la temperatura es un factor limitante importante que puede afectar negativamente al intercambio gaseoso en el algarrobo y, a pesar de que el gradiente de temperatura presente entre nuestras zonas de estudio es reducido (1- 2 °C), éste se relacionó con algunas variables de intercambio gaseoso.

Los modelos más optimistas de cambio climático estiman un incremento de la temperatura global de 1 a 2 ºC (Fischer y Knutti, 2015). Debido a la inercia térmica del Océano Pacífico y al gradiente climático generado en la costa por la corriente de Humboldt, se espera que este incremento de la temperatura derive en un aumento progresivo de las precipitaciones (Bates et al., 2008). Aunque el incremento de la precipitación de verano favorezca la actividad fisiológica del algarrobo, es aún incierto si es suficiente para compensar el incremento de la temperatura. Considerando que el ciclo climático anual contiene además 8-9

meses sin precipitaciones, es de esperar que un incremento de la temperatura y de la precipitación tenga un efecto perjudicial para la fotosíntesis y la regulación hídrica.

Estos modelos también estiman un aumento en la frecuencia de los eventos de El Niño (Wang et al., 2017). Nuestros resultados sugieren que las poblaciones de algarrobo presentan una respuesta plástica frente a la disponibilidad de agua, y serían capaces de crecer y sobrevivir durante la fase húmeda y seca del ciclo climático regional. Sin embargo, la plasticidad de las características fisiológicas asociadas al transporte de agua es menor en las poblaciones con mayor estrés ambiental. Si las temperaturas siguen aumentando en las poblaciones de Ignacio Tavara y Locuto, la plasticidad de la eficiencia en el uso del agua podría disminuir en futuras generaciones y provocar la pérdida de la variabilidad funcional de estas poblaciones y su resiliencia.

Variabilidad intraespecífica de rasgos funcionales del algarrobo

Mientras que la fase húmeda representa un evento extremo que requiere una respuesta plástica, la fase seca es un proceso selectivo que limita la plasticidad y favorece procesos de selección (Lande, 2009). La plasticidad fenotípica es una respuesta fisiológica a condiciones variables, pero sólo tiene lugar cuando existe suficiente variabilidad genética (Gratani, 2014) y la especie se enfrenta a condiciones climáticas fluctuantes (ver anexo Anexo 3). A través de los datos de campo del ***capítulo 4*** encontramos una alta variabilidad intraespecífica en los rasgos funcionales de la hoja, la cual tiene relación con la alta plasticidad fenotípica que encontramos en las poblaciones de algarrobo en el experimento de invernadero (***Capítulo 3***) y con los resultados dendrocronológicos (***Capítulo 2***).

Es de resaltar que la variabilidad de los rasgos funcionales de la hoja en el algarrobo sigue la misma tendencia que el espectro económico de la hoja a nivel interespecífico (LES, leaf economics spectrum, con más de 2500 especies) (Wright et al., 2004), cubriendo más de la mitad de la variabilidad del LES (Fig. 4) (***Capítulo 4***). Esto además sugiere la existencia de un compromiso entre la composición de la hoja y el intercambio gaseoso en el algarrobo, donde plantas

con más peso específico foliar (LMA) tendrán una menor tasa fotosintética por unidad de peso foliar y una mayor conservación de los recursos, mientras que plantas con menos LMA tendrán más tasa fotosintética por unidad de peso foliar y un mayor consumo de los recursos. El capítulo 4 mostró que el eje del PCA relacionado con el LES y la estrategia de uso de recursos representaba el 28% de la variabilidad de los rasgos funcionales de la hoja, mientras que la regulación hídrica cubría un 17% (Fig. 5).

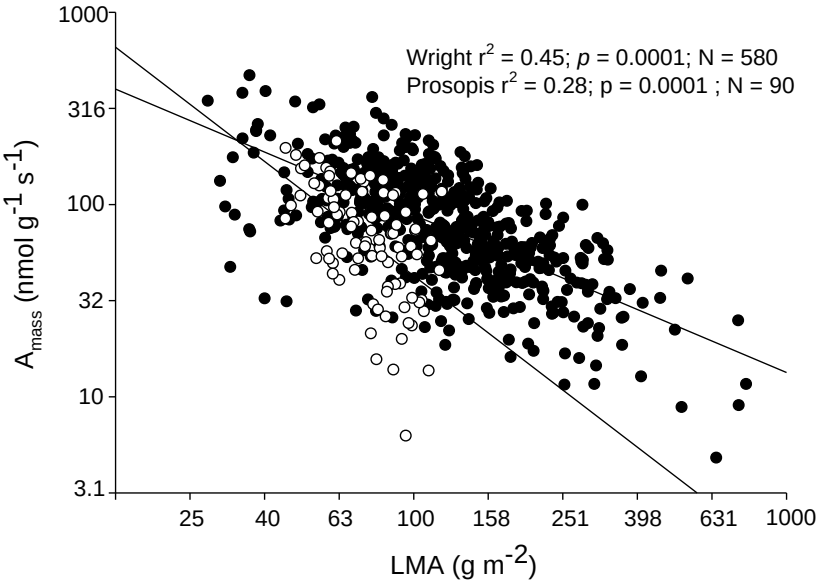

Figura 4. Análisis de regresión entre el peso específico foliar (LMA) y la tasa fotosintética neta por unidad de peso foliar (A_{mass}). Los puntos negros pertenecen al espectro económico global de la hoja (LES, Wright et al. 2004), y los puntos blancos representan los datos obtenidos de las poblaciones de algarrobo (Capítulo 4).

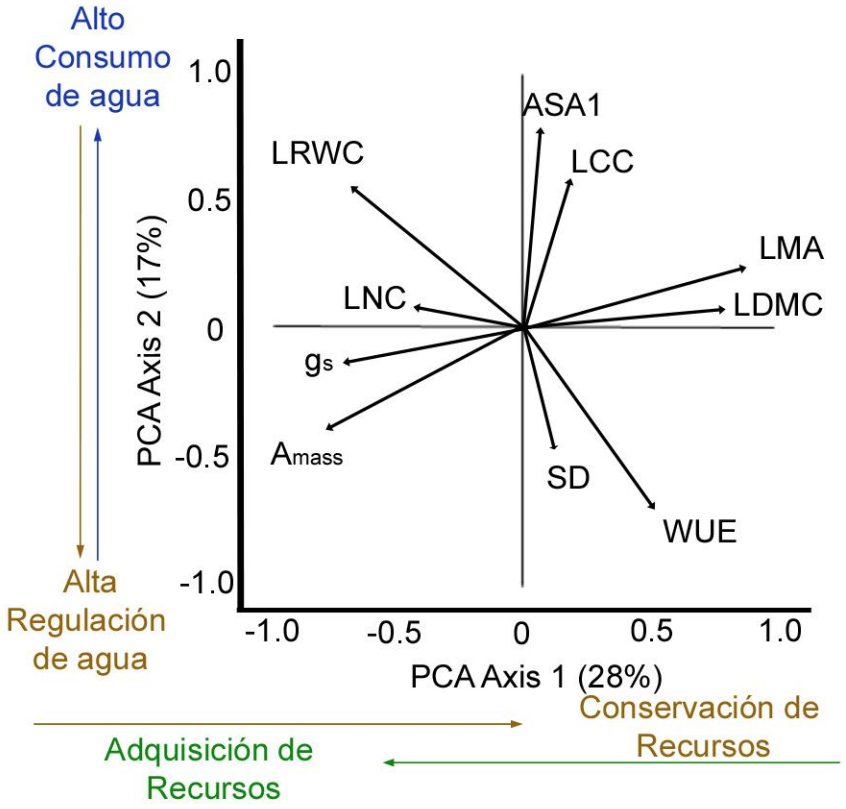

Figura 5. Análisis de componentes principales de los rasgos funcionales en algarrobo. ASA1: Área estomática del envés, LCC: concentración de carbono en hoja, LDMC: Contenido en materia seca. LMA: Peso específico foliar, LNC: concentración de nitrógeno en hoja, LRWC: Contenido relativo de agua en hoja, A_{mass}: Tasa fotosintética neta por unida de peso foliar, gs: Conductancia estomática, SD: Densidad estomática, WUE: Eficiencia en el uso del agua.

Variabilidad intraespecífica del algarrobo a diferentes escalas (árbol, parcela y población)

Las causas de la variabilidad intraespecífica pueden descomponerse según diferentes escalas espaciales. A nivel poblacional, factores climáticos como la temperatura o la precipitación pueden ser responsables de la variabilidad de intraespecífica. En cambio, a nivel de parcela o a nivel de árbol, la variabilidad genética, edáfica y micro-climática pueden jugar un papel más importante (Jung et al., 2010). La descomposición de la varianza de los rasgos funcionales de la hoja de algarrobo en relación a la escala espacial (***Capítulo 4***) indica que la variabilidad a nivel de parcela y árbol es más importante (70%) que la variabilidad poblacional (30%) (Fig. 6). Esto puede explicar porque la

precipitación media anual no se correlacionó con ningún rasgo funcional de la hoja, mientras que la temperatura media anual si se correlacionó con algunas variables, principalmente aquellas relacionadas con la regulación hídrica.

Por otro lado, la variabilidad de la fertilidad y características del suelo también fue significativamente alta (***Capítulo 5***). Los nutrientes en el suelo presentaron una fuerte correlación entre ellos, de modo que las poblaciones de algarrobo con mayor concentración de N, fueron también las que presentaban mayor contenido en P, C, Mg, Mn, Ca y K. Más del 60% de la variabilidad de los nutrientes estuvo contenida en el primer eje del análisis de componentes principales (PCA), lo cual sugiere que la variabilidad tiene un origen común. Sin embargo, la fertilidad del suelo no se correlacionó con la variabilidad climática o la distribución geográfica de las poblaciones, y podría ser una fuente de variabilidad independiente que afecta al funcionamiento del algarrobo.

Al igual que en los rasgos funcionales de la hoja, la descomposición de la variación de los nutrientes en suelo indicó que sólo un 38% es explicada a nivel poblacional (Fig. 6). De modo que, la variabilidad local es más importante también en este caso, y sumado a la variabilidad intrínseca del algarrobo, podría explicar por qué la variabilidad de los nutrientes en hoja es de 65 % a nivel de árbol (Fig. 6). Por tanto, múltiples procesos a nivel de micro-escala pueden ser responsables de la alta variabilidad en nutrientes y rasgos funcionales.

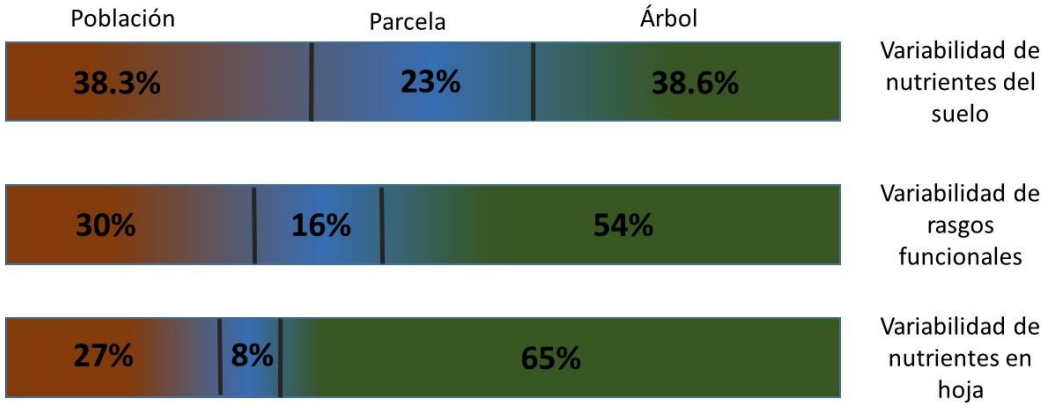

Figura 6. Descomposición de la varianza según la escala espacial para los nutrientes en suelo, los rasgos funcionales y los nutrientes en hoja.

En general, la alta variabilidad del algarrobo podría estar relacionada con la escasa frecuencia de encontrar relaciones entre variables a nivel

intrapoblacional. Sin embargo, en algunos casos, se han detectado algunas relaciones interesantes a nivel intrapoblacional. Así, por ejemplo, en el caso de la isla de fertilidad (***Capítulo 6***), las diferencias interpoblacionales permitieron observar que los árboles de Rinconada (la población más cercana a la costa) tenían un efecto superior a la media sobre la concentración de nutrientes en el suelo (Fig. 7). Igualmente, en el estudio de la acumulación foliar de Mn (***Capítulo 5***) encontramos una diferente respuesta entre poblaciones, de forma que Ñapique seco (la zona más desértica) presentaba mayores concentraciones de Mn en la hoja en relación a los nutrientes en el suelo en comparación con la media regional. También se observó como en Piura (la única plantación artificial estudiada) presentaba correlaciones significativas entre el tamaño del árbol y la concentración de C y N en suelo. Esto posiblemente se deba a que los árboles en esta población tienen la misma edad, y han seguido el mismo sistema de manejo, lo cual ha reducido otras causas de variabilidad fenotípica poblacional. Por tanto, es necesario mantener un alto número de réplicas en zonas de alta variabilidad para obtener resultados significativos, salvo en casos extremos, donde los efectos son suficientemente intensos para detectar diferencias.

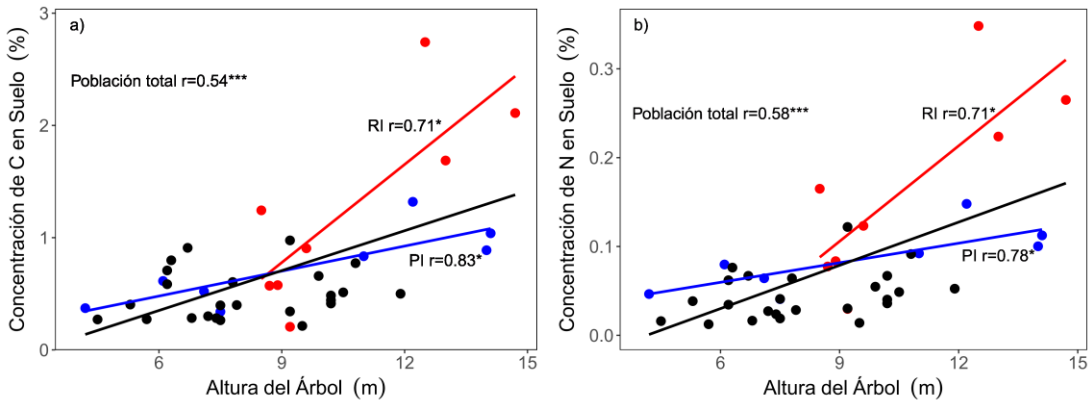

Figura 7. Relación entre la altura del árbol y la concentración de C (**a**) y N (**b**) en el suelo. La línea negra indica la relación en toda la región, mientras que la línea roja y azul indica la relación en las poblaciones de Rinconada y Piura, respectivamente.

Relaciones suelo – planta sobre la nutrición vegetal

A través del estudio para evaluar el efecto de "isla de fertilidad" (***Capítulo 6***) encontramos que el algarrobo tiene un efecto significativo sobre la concentración de nutrientes en el suelo. Existe una relación negativa entre la concentración de nutrientes y la distancia al árbol; sin embargo, el efecto es muy bajo (valores de R^2 en torno al 0.02), por tanto, la distribución espacial del algarrobo, por sí solo, no es un factor determinante sobre la variabilidad en la concentración de los nutrientes del suelo. Aunque el efecto de isla de fertilidad en algarrobo ha sido ampliamente estudiado, hay algunos casos donde la distancia al árbol no ha sido un factor determinante (Deans et al., 2003; Kahi et al., 2009). En cambio, el tamaño del árbol y la concentración de nutrientes en la hoja sí se correlacionaron con la concentración de nutrientes en el suelo, por tanto la variabilidad de tamaño de los individuos de algarrobo y la calidad del follaje son una fuente adicional de la variabilidad de nutrientes del suelo (Gallaher y Merlin, 2010), y esto podría explicar el importante porcentaje de varianza explicado (en torno al 65%) a nivel de árbol.

Así como la concentración de nutrientes en el suelo ha mostrado estar relacionada con las características foliares y de tamaño del algarrobo, la adquisición de nutrientes por parte de la planta ha mostrado estar relacionada con las características del suelo. El pH se correlacionó negativamente con las relaciones de N/C y P/C en la hoja, dos de los nutrientes más limitantes en las plantas (Hedin, 2004). Podríamos deducir que un pH básico estaría asociado a una limitación en la adquisición de estos nutrientes, aunque no sería el caso para la adquisición de Ca o Cu. Estos niveles son comunes en zonas áridas como la zona estudiada (Alban et al., 2002; Pasiecznik et al., 2001); por tanto, es de esperar que el algarrobo presente modificaciones especiales para aumentar la movilidad de nutrientes hacia la planta. Por ejemplo, la escasez de nutrientes en zonas áridas puede ser compensada por una reducción local del pH del suelo a fin de incrementar la movilidad de algunos elementos, como el P (Lambers et al., 2015). Esta disminución no sólo favorece la disponibilidad de nutrientes limitantes, sino también la absorción del Mn. Este elemento es almacenado en la vacuola, y dado que no es limitante, no suele ser translocado durante la senescencia de la hoja. Nuestros resultados muestran que la relación Mn/C en

hoja se correlaciona negativamente con 7 de los 10 elementos minerales analizados en el suelo, indicando que en suelos pobres en nutrientes las plantas tienen una alta relación Mn/C. Por tanto, el índice Mn/C o bien la concentración de Mn en hoja puede ser un indicador eficiente para determinar la existencia de estos mecanismos a nivel de la raíz para aumentar la absorción de nutrientes.

La acumulación de Mn en la hoja podría tener un efecto sobre la calidad de la hojarasca, de modo que hojas con alto contenido en Mn incorporarían más Mn al suelo como parte del efecto de la isla de fertilidad. Si la actividad de la raíz continuara alterando el pH, es posible que el ciclo suelo-planta del Mn mantenga una retroalimentación positiva que pudiera alcanzar niveles tóxicos. Sin embargo, éste es un escenario poco probable porque el Mn requiere concentraciones muy altas para ser tóxico (200 a 3500 mg kg^{-1}), y el algarrobo, en algunos casos, ha demostrado ser capaz de acumular metales pesados tóxicos sin perjuicio sobre el crecimiento (Buendía-González et al., 2010; Gardea-torresdey et al., 2005). Además, los valores máximos de concentración de Mn en el suelo de las zonas estudiadas es bajo (en torno al 28 mg kg^{-1}).

Limitaciones del estudio

El estudio del efecto de la variabilidad climática sobre el crecimiento y la variabilidad intraespecífica presenta algunas limitaciones que pudieron afectar a la obtención de más resultados durante la realización de esta tesis. Entre ellas están:

1. ***Ausencia de información climática nacional de detalle***. El uso de bases de datos globales como la CRU (climate research unit) y WorldClim ha permitido estudiar el efecto de la variabilidad climática. Sin embargo, estas bases de datos solo tienen en cuenta factores globales como la precipitación y la temperatura sin tener en cuenta factores locales como la corriente Walker (que controla el comportamiento de los vientos), la radiación o la presencia de la capa de inversión térmica que retiene la humedad por debajo de los 100 m de altura. La falta de datos ambientales a nivel de parcela o árbol también limita nuestro análisis de la

variabilidad, dado que no podemos determinar con precisión las fuentes de variación a micro-escala.

2. ***Duración del experimento de invernadero***. El rápido crecimiento de las plantas durante el experimento de invernadero (más de 1 m de altura en 2 meses) adelantó la fase de la cosecha. Este periodo corto de crecimiento podría haber reducido las diferencias entre tratamientos que podrían haberse detectado considerando un periodo de experimentación más prolongado.

3. ***Ausencia de medidas adicionales en el efecto de la isla de fertilidad***. La producción de hojarasca, la respiración del suelo, y la actividad de la raíz son factores que no se midieron en el estudio de la isla de fertilidad, y que podrían haber sido las causas de las diferencias entre poblaciones.

4. ***Intensidad del gradiente climático***. Un gradiente climático latitudinal tendría más variabilidad en la temperatura del aire, en comparación con el gradiente longitudinal que se usa en esta tesis. Esto podría esclarecer el papel de la temperatura sobre la variabilidad funcional de manera independiente a la precipitación.

5. ***Restricciones en el uso de las poblaciones.*** En algunos capítulos no fue posible tener en cuenta las 8 poblaciones del gradiente climático. La degradación del bosque seco y la tala ilegal nos impidió trabajar en más de 3 poblaciones en el capítulo 2 dado que la obtención de discos de madera requería talar arboles. En el capítulo 3 excluimos una población debido a la ausencia de semillas en la zona. También en el capítulo 6 excluimos 3 poblaciones por problemas logísticos y experimentales.

Aspectos aplicados

Los resultados obtenidos en esta tesis arrojan también aspectos aplicados sobre la conservación y uso de los bosques de algarrobo. Esto puede permitir la mejora de la calidad de vida de las poblaciones rurales que habitan en él, así como la investigación científica en zonas áridas. Entre los posibles aspectos aplicados están:

1. ***Uso del algarrobo en la dendroarqueología***. Los resultados obtenidos demuestran que el crecimiento de los anillos es un buen indicador de la precipitación de verano. Numerosos monumentos arqueológicos pre-incaicos y coloniales han sido construidos usando troncos de algarrobo como columnas y dinteles. La alta densidad de la madera (1.1 g cm^{-3}) le ha otorgado la durabilidad necesaria para conservarse a la intemperie por más de 2000 años. Por tanto, el uso de la dendrocronología en restos arqueológicos podría permitir la reconstrucción climática del pasado. Esto no sólo nos permitiría reconstruir el contexto ambiental de estas civilizaciones, sino que además nos permitiría construir la historia del ENSO en el tiempo.

2. ***Conservación de la variabilidad intraespecífica***. La baja biodiversidad de las zonas áridas suele estar compensada por una alta variabilidad genética. Los resultados obtenidos demuestran que el algarrobo presenta una alta variabilidad intraespecífica, la cual permite afrontar la gran variabilidad climática y edáfica. Por tanto, los resultados de esta tesis apoyan la importancia de programas de conservación del germoplasma de estas poblaciones.

3. ***Bases para el estudio del cambio climático***. Se estima que el calentamiento del planeta aumente la temperatura del Océano Pacífico y la corriente de Walker. Esto aumentaría la intensidad y la frecuencia del ENSO así como las precipitaciones en la fase seca del clima. Los resultados obtenidos permiten establecer una línea base sobre la cual futuros proyectos pueden estimar el impacto del cambio climático sobre el crecimiento y la variabilidad intraespecífica del algarrobo.

4. ***Uso de la concentración de Mn foliar como un indicador de fertilidad***. La concentración de Mn en hoja se correlaciona negativamente con la concentración de C, N, Mg, Ca, Cu, Fe y el Zn en suelo. Por tanto, en suelos pobres de nutrientes se encuentra que las hojas acumulan Mn. Además, la concentración de Mn foliar se correlaciona negativamente con la conductividad eléctrica del suelo. Por tanto, la concentración de Mn foliar podría ser usado como un indicador de la fertilidad y movilidad de los nutrientes del suelo a la planta.

5. ***Uso de la isla de fertilidad de algarrobo en sistemas agroforestales.*** Los programas de reforestación en zonas áridas de Perú tienen en cuenta el algarrobo como un elemento importante de la recuperación del terreno. Nuestros resultados sugieren que el efecto de la isla de fertilidad cambia significativamente según el tamaño del árbol y la estructura de la hoja, por tanto, es importante tener en cuenta para evaluar el efecto de la isla de fertilidad.

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Conclusiones

1. El algarrobo es una especie plástica capaz de sobrevivir a largos periodos secos e incrementar su crecimiento durante precipitaciones extremas. El algarrobo es capaz de crecer hasta 4 veces más durante años del ENSO (fase húmeda) en comparación con años normales (fase seca) (***Capítulo 2***).

2. El crecimiento del algarrobo presenta una alta sensibilidad a la variabilidad climática local, la cual está controlada por la temperatura del mar en la costa Norte (región Niño 1+2). El crecimiento radial se correlacionó positivamente con el indicador costero de la temperatura del mar (r = 0.67), la precipitación (r = 0.65) y la temperatura de verano (r = 0.23) (***Capítulo 2***).

3. Las poblaciones de algarrobo presentan una plasticidad diferente dependiendo de los rasgos estudiados en respuesta a la disponibilidad hídrica. Sin embargo, dicha plasticidad, en general, no se relaciona con la variabilidad climática local (***Capítulo 3***).

4. La plasticidad de la eficiencia en el uso del agua fue el único rasgo que presentó una correlación negativa con la precipitación anual (r = -0.84) y una correlación positiva con el índice estandarizado de sequía (SPEI) (r = 0.83) (***Capítulo 3***).

5. Durante una alta disponibilidad de agua, el crecimiento se relaciona positivamente con la proporción de la raíz (r = 0.47) y negativamente con el peso específico foliar (r = - 0.37), lo cual incrementa la eficiencia en el uso del agua (r = 0.97) y la evapotranspiración (r = 0.93) y (***Capítulo 3***).

6. Los rasgos funcionales de la hoja en el algarrobo presentan una alta variabilidad intraespecífica que de forma muy similar sigue la tendencia del espectro económico global de la hoja (***Capítulo 4***).

7. La temperatura media anual de las poblaciones estuvo negativamente relacionada con las variables regulación hídrica de la hoja, correlacionándose negativamente con el contenido relativo de agua en hoja (r = -0.82) y el tamaño del estoma (r = -0.71), y positivamente con la eficiencia en el uso del agua (r = 0.91) (***Capítulo 4***).

8. La variabilidad del suelo de los bosques de algarrobo está explicada mayormente (65%) por un eje que representa la fertilidad del suelo, y se

relaciona positivamente con la relación P/C (r = -0.18) y negativamente con la relación Mn/C (r = 0.21) en la hoja (***Capítulo 5***).

9. Las características del suelo como el pH y la conductividad eléctrica está relacionada con la absorción de nutrientes en las poblaciones de algarrobo. Así, el pH del suelo se correlacionó negativamente con la relación N/C y P/C de la hoja, y positivamente con la relación Ca/C y Cu/C de la hoja, mientras que la conductividad eléctrica se correlacionó negativamente con la relación Fe/C y Mn/C de la hoja, y positivamente con la relación K/C y Cu/C del suelo (***Capítulo 5***).

10. La concentración de Mn o la relación de Mn/C en la hoja se correlacionó negativamente con la concentración de C, N, Ca, Mg, Fe, Cu y Zn del suelo, así como con la conductividad eléctrica. Por ello, ha mostrado ser un indicador adecuado de suelos infértiles (***Capítulo 5***).

11. El tamaño del árbol y la composición química de la hoja se correlacionaron positivamente con la concentración de nutrientes en el suelo cercano al árbol. Por tanto, el efecto de la isla de fertilidad depende de las características del algarrobo, y no tanto de su proximidad (***Capítulo 6***).

12. El efecto de la isla de fertilidad fue diferente entre poblaciones. Esto puede deberse a un incremento en la actividad microbiana o una mayor producción de biomasa vegetal en zonas con características ambientales favorables (mayor humedad relativa y menor temperatura) (***Capítulo 6***).

Agradecimientos

Todo empezó cuando estaba en segundo de carrera y Carmen Galán mencionó que el algarrobo era una especie representativa de la zona Mediterránea. No pude sino contener mi ira hasta el final de la clase para acércame y decirle que el algarrobo era una especie nativa de Piura, la ciudad donde yo crecí. Me tomó una semana darme cuenta que estaba equivocado, por supuesto, y que ambas especies (*Ceratonia siliqua* y *Prosopis pallida*) compartían el mismo nombre común porque Pizarro y sus hombres vieron lo que parecía la misma especie, y le pusieron el mismo nombre, durante la conquista y descubrimiento de Perú. En mi afán por esclarecer mi error termine descubriendo que el algarrobo peruano es uno de los elementos más importantes de las zonas áridas de Perú y Sudamérica en general. A pesar de ello, no había suficiente investigación para entender su funcionamiento y complejidad. En ese momento decidí que no podía dejar que el algarrobo fuese "el gran ignorado", y tenía que hacer lo que estuviese en mis manos por aportar algo.

Ha sido un largo camino desde entonces y no podría haberlo logrado solo. En orden cronológico debo agradecer a:

Carmen Galán por escucharme y creer en mí. Era solo un estudiante con ganas de hacerlo todo, y ella supo darme el apoyo y la guía necesaria para que persiguiera este sueño.

Rafael Villar por darme un espacio en su equipo para aprender lo que realmente es la investigación científica y por ofrecerme lo que fue mi primer trabajo como investigador.

Rafael Navarro por guiarme de regreso a Latinoamérica y apoyarme en la creación de un grupo de trabajo que permita crear investigación en zonas áridas en Perú.

A Gastón Cruz, Nora Grados y Rodolfo Rodríguez por darme un espacio y una voz en la Universidad de Piura para poner en marcha esta tesis y el proyecto en el que se enmarca.

A Antonio Mabres por creer en mí, y en el algarrobo como elemento crucial en el futuro del bosque seco.

A la Universidad de Córdoba y la Universidad de Piura por su ayuda logística y científica a lo largo de todas las pericias que implica llevar un proyecto conjunto a pesar de las distancias.

A Vildal Barrón por su ayuda en los análisis edafológicos, y a Luis Urbina, Luis Sullon, Celinda Peña, Marco Balcazar y Lorena Huiman por su participación en la toma de datos y soportar a mi lado las penurias del desierto.

A Dalila, Fabiola y Janet por su continua ayuda en el laboratorio de Química de la Universidad de Piura.

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Por supuesto, nada de esto hubiera sido posible sin el apoyo de mis padres, en especial de mi madre, quien ha sacrificado su vida por el bienestar de sus hijos.

Por último y más importante, debo agradecer la paciencia de mi esposa Beatriz quien ha atravesado océanos para estar a mi lado mientras perseguía molinos de viento. Gracias por creer en mí.

Anexo 1

Descripción de las poblaciones forestales de algarrobo en la región norte

Se seleccionaron 7 zonas de bosque seco de algarrobo representativas de la región siguiendo el gradiente de temperatura y precipitación de la costa al interior (Fig. 1 y tabla 1). Debido a la alta variabilidad ambiental encontrada en la zona de Ñapique, dividimos esta zona según su distancia a la laguna allí presente, siendo "Ñapique Seco" la zona más lejana, y "Ñapique Húmedo" la zona más cercana a la laguna. En total, se estudiaron 8 poblaciones de algarrobo.

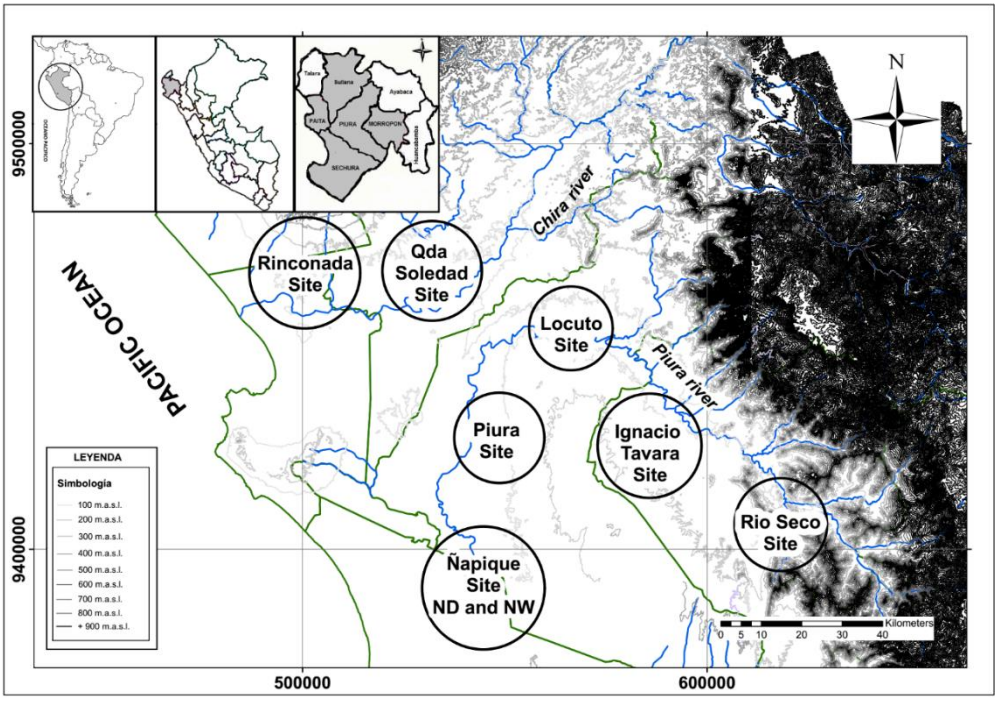


Figura 1. Distribución geográfica de las zonas de bosque seco elegidas para este estudio.

Table 1. Descripción climática (periodo: 1950-2000) y localización (UTM) de las poblaciones de algarrobo incluidas en este estudio. Temperatura anual media (MAT), precipitación anual media (MAP), el índice estandarizado de precipitación-evapotranspiración (SPEI) y la desviación estándar fueron obtenidas de la base de datos de la CRU - Global Climate data (http://www.cru.uea.ac.uk/). Las poblaciones están ordenadas por la precipitación media anual.

Zona	MAP (mm)	MAT (ºC)	SPEI	Altitud (m a.s.l.)	Longitud 17 M	Latitud
Ñapique Seco	7.65 ± 8	22.95 ± 0.71	-0.08 ± 0.79	15	560606	9405427
Ñapique Húmedo	7.65 ± 8	22.95 ± 0.71	-0.08 ± 0.79	15	560606	9405427
Rinconada	18.48 ± 24	22.44 ± 0.73	-0.14 ± 0.78	77	513373	9457293
Piura	40.87 ± 41	23.56 ± 0.7	-0.17 ± 0.68	40	532471	9433785
Quebrada Soledad	122 ± 155	23.18 ± 0.44	-0.17 ± 0.5	61	519339	9455070
Ignacio Tavara	178.48 ± 123	24.11 ± 0.65	-0.22 ± 0.48	153	596277	9434052
Locuto	276.94 ± 199	23.58 ± 0.64	-0.2 ± 0.53	69	584564	9422283
Rio Seco	316.11 ± 148	20.32 ± 0.64	-0.17 ± 0.42	232	621417	9414217

Dentro de cada zona se eligieron 3 áreas de muestreo, alejadas aproximadamente 1265 m entre sí para cubrir la mayor variabilidad posible

dentro de cada zona y no tener problemas de seudoreplicación. Dentro de cada área se eligieron 5 árboles adultos distancias aproximadamente 100 m entre sí, y en buen estado fitosanitario a modo de unidades experimentales independientes.

A continuación se describen las distintas zonas estudiadas.

Bosque seco "La Rinconada": Ubicado a 13 km de la costa, es la población con mayor cobertura forestal de la región. Además de *P. pallida*, la vegetación está compuesta de especies arbustivas como el zapote (*Colicodendrum scabridum*) y el faique (*Acacia macracantha*), sin presencia de pastizales. Debido a su cercanía al océano presenta una elevada humedad atmosférica, y baja evapotranspiración, y debido al comportamiento de las condiciones climáticas antes descritas, es también una de las zonas con menor precipitación. El suelo es arenoso, con una gran acumulación de materia orgánica en forma de hojarasca y heces de venados y zorros.

Bosque seco "Quebrada Soledad": Ubicado a 28 km de la costa, es un bosque seco formado en el antiguo recorrido del rio Soledad. Es parte de la zona de amortiguamiento de la empresa Maple Etanol S. A., la cual no contempla ningún plan de manejo o aprovechamiento forestal. La zona se encuentra cercada y protegida de los herbívoros. Además de *P. pallida*, la vegetación está compuesta de especies arbustivas como el zapote y el faique, sin presencia de pastizales. El suelo es arenoso y rocoso.

Bosque seco de Ñapique (Ñapique Seco y Ñapique Húmedo): Ubicado a 18 km de la costa, rodea la laguna Ñapique en la desembocadura del rio Piura, en la entrada al desierto de Sechura. Debido al bajo contenido de nutrientes en esta zona, las características de la vegetación cambian según su distancia a la laguna, la cual además puede cambiar significativamente de tamaño durante el ENSO (Fig. 4). Durante la fase húmeda, la población de "Ñapique Húmedo" puede encontrarse sumergida hasta 50 cm, mientras que la población de "Ñapique Seco" al estar más alejado de la laguna, se encuentra siempre fuera del área de impacto de la laguna. En Ñapique Húmedo podemos encontrar vegetación herbácea acompañante, mientras que Ñapique Seco solo presenta tamarix (*Tamarix aphilla*) como vegetación acompañante.

Bosque seco de "Piura": Ubicado a 43 km de la costa, es un bosque seco formado en las cercanías del Rio Piura, y parcialmente reforestado en

1980 por la Universidad de Piura dentro de un plan de manejo exhaustivo. Además del algarrobo, la vegetación presenta una baja proporción de zapotes y faiques.

Bosque seco de "Locuto": Ubicado a 80 km de la costa, solía ser uno de los bosques secos rurales más productivos de la región, siendo además el asentamiento de numerosas empresas productoras de algarrobina (subproducto obtenido del fruto). Debido a la orografía del terreno, esta población es considerada parte del "Alto Piura" junto con Ignacio Távara y Rio Seco, presentando fuertes fluctuaciones en la precipitación durante el ENSO.

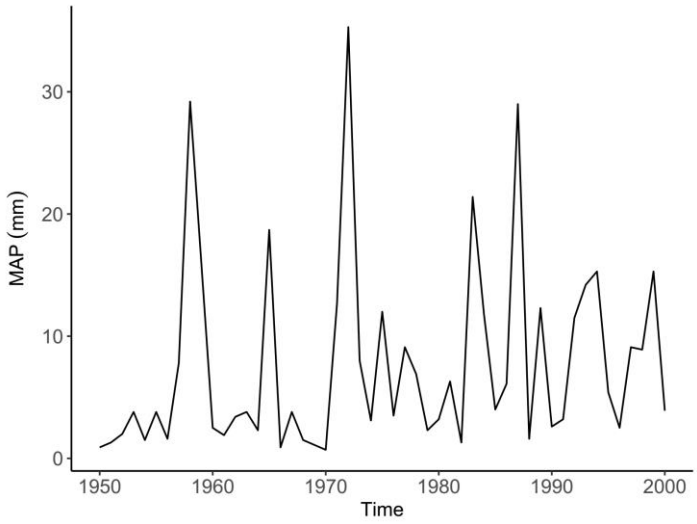
Bosque seco de "Ignacio Távara": Ubicado a 88 km de la costa, es la zona rural con mayor número de algarrobos de la región, y el hogar de las empresas de algarrobina y miel más grandes de la región. Además del faique y el zapote, es posible encontrar también overol (*Cordia lutea*) y cun cun (*Vallesia glabra*) en esta zona. Debido a la baja productividad del bosque en los últimos 10 años, la actividad rural ha empezado a migrar hacia una agricultura intensiva.

Bosque seco de "Rio Seco": Ubicado a 114 km de la costa, es la zona de mayor precipitación dentro del estudio. Aunque el gradiente climático es notorio de oeste a este a lo largo de todas las zonas de estudio, Rio Seco presenta la menor temperatura de la región debido a los vientos del este provenientes de las laderas de la sierra. Por ello, esperamos que la información proveniente de esta población nos ayude a separar el efecto de la temperatura y la precipitación sobre las variables estudiadas en esta tesis. Además, esta zona presenta un alto contenido en limo (14%), lo cual lo hace un suelo franco-arenoso, facilitando la retención de nutrientes y metales pesados.

Anexo 2

Variabilidad climática en las zonas de estudio

Ñapique


MAP (mm)
30
20
10
0
1950
1960
1970
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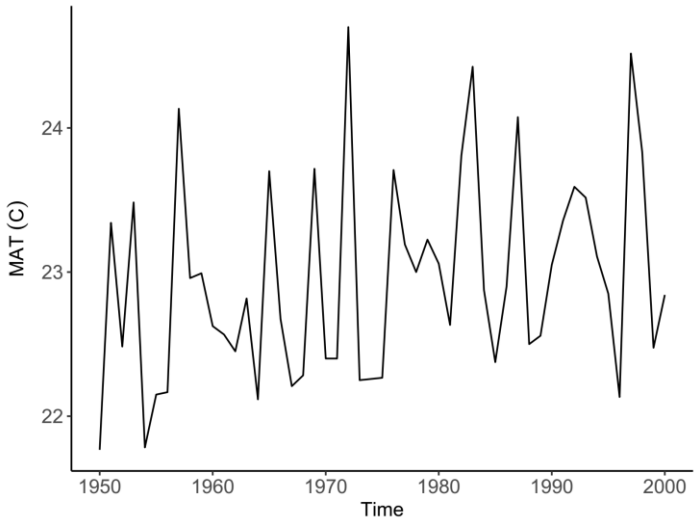
2000
Time


MAT (C)
24
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22
1950
1960
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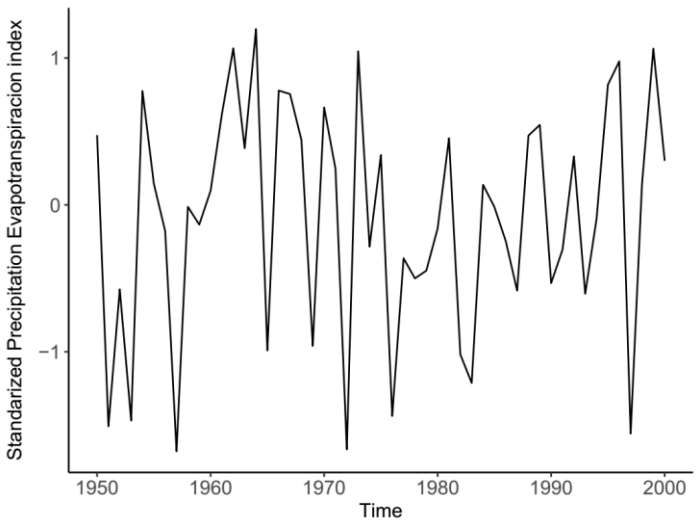
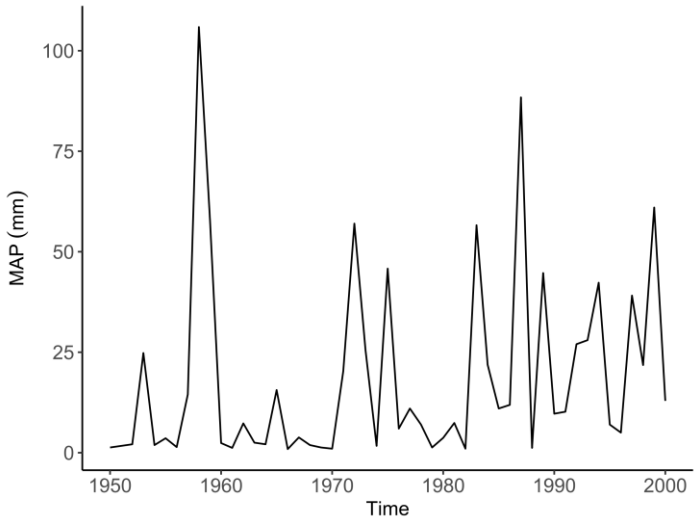
1980
1990
2000
Time


Standarized Precipitation Evapotranspiracion index
1
0
−1
1950
1960
1970
1980
1990
2000
Time

Rinconada


MAP (mm)
100
75
50
25
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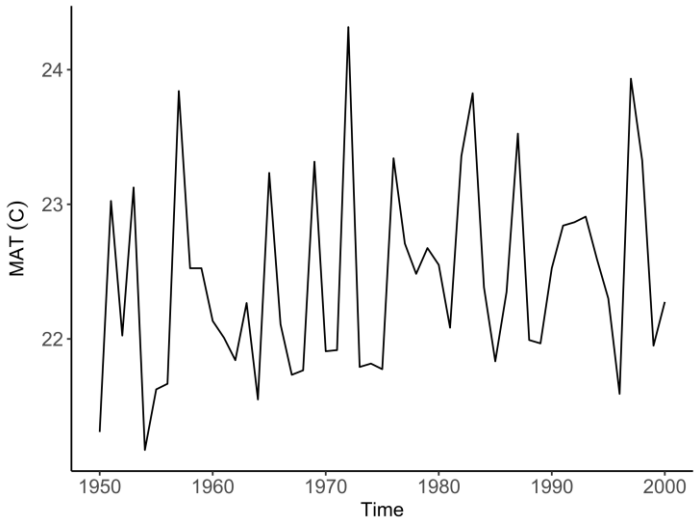
Time


MAT (C)
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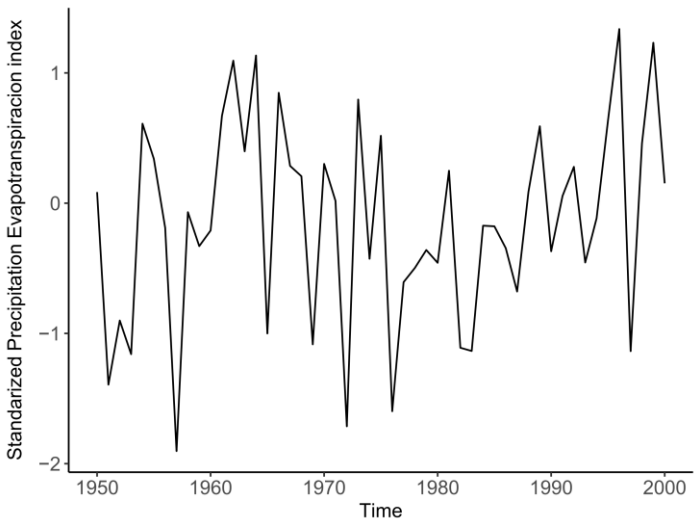
Standarized Precipitation Evapotranspiracion index
1
0
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1950
1960
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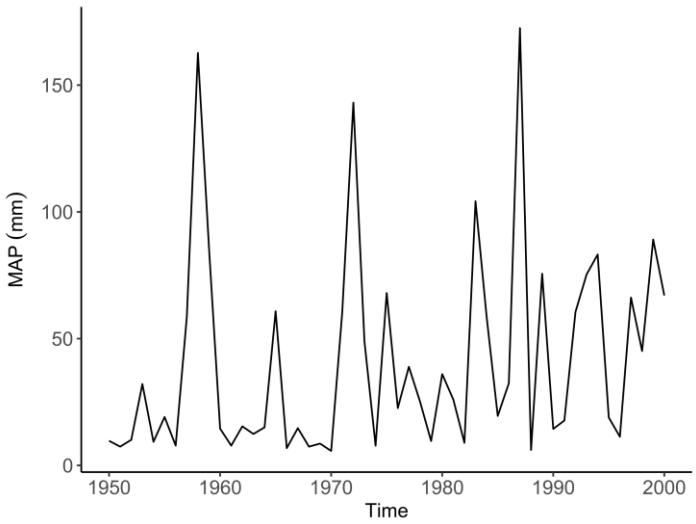
Time

Piura


MAP (mm)
150
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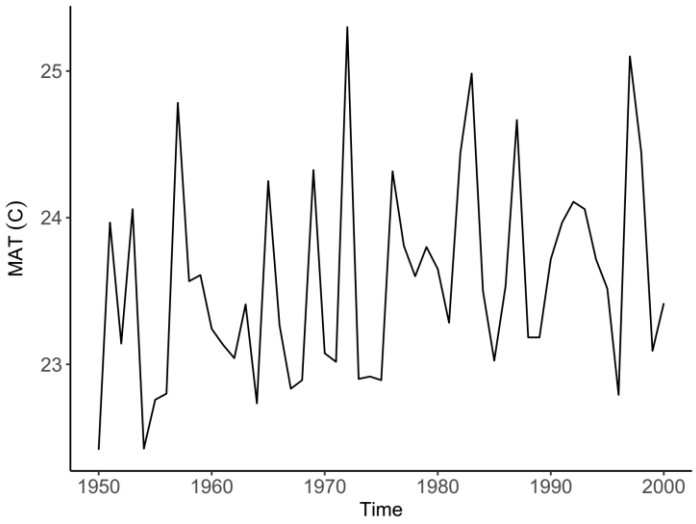
MAT (C)
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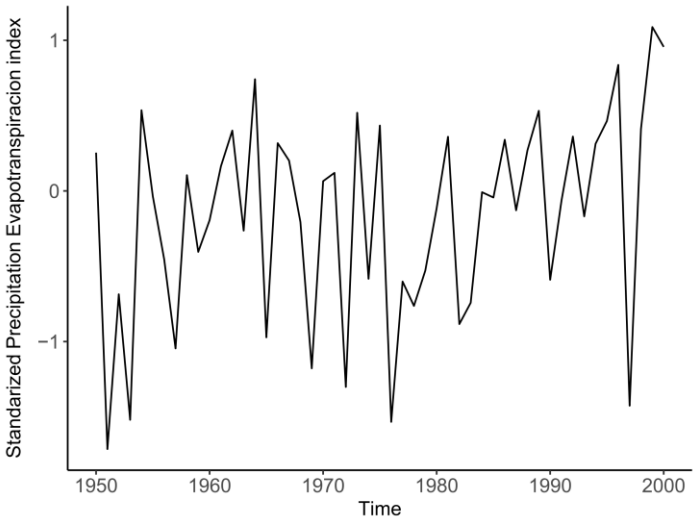
Standarized Precipitation Evapotranspiracion index
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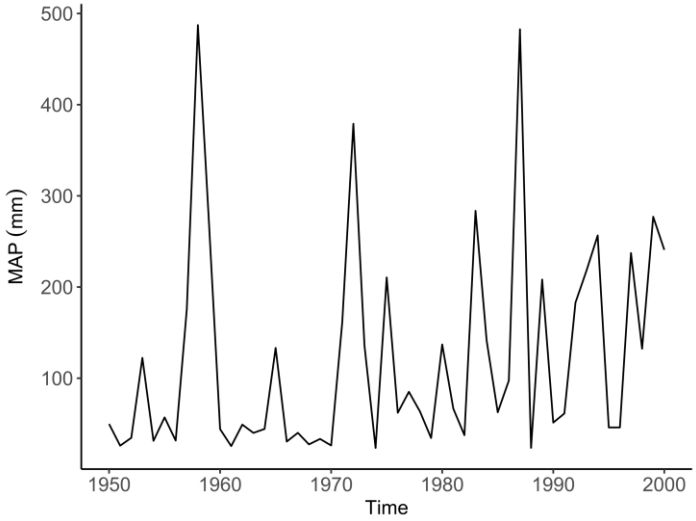
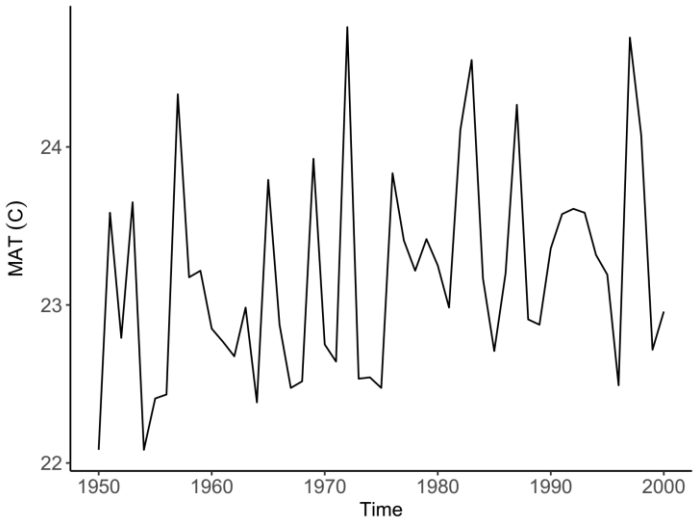
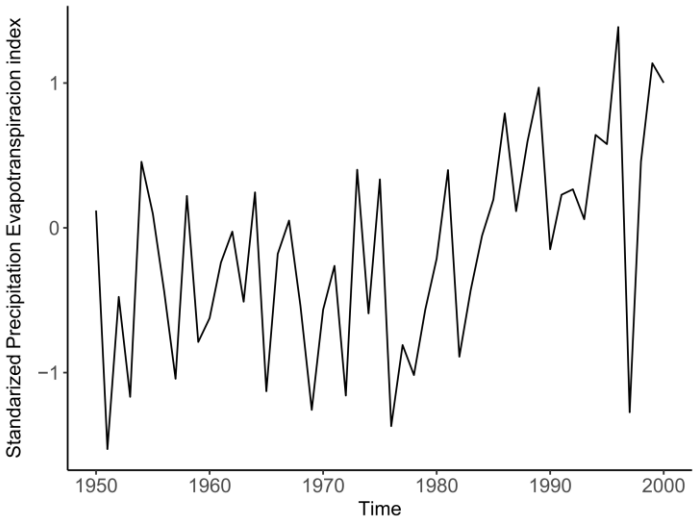
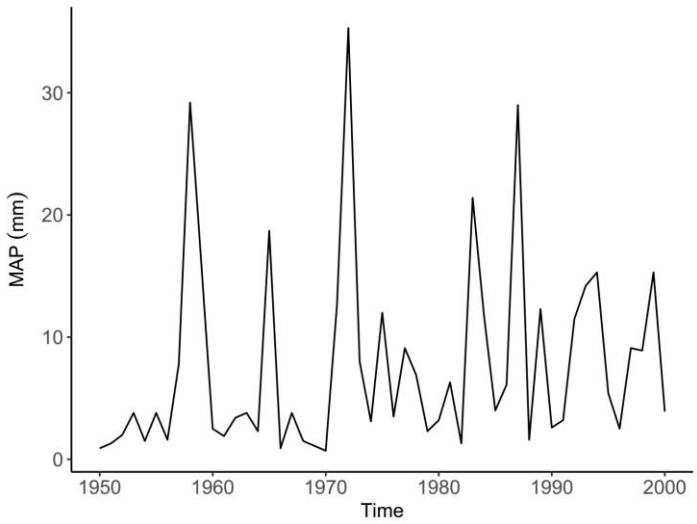
Quebrada Soledad

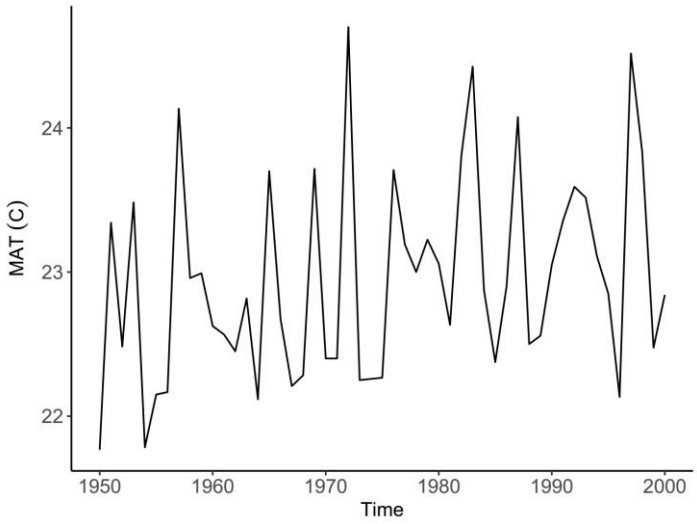


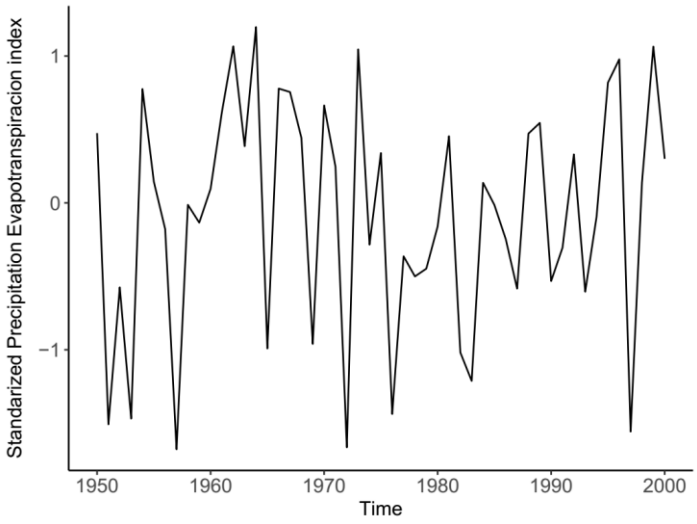




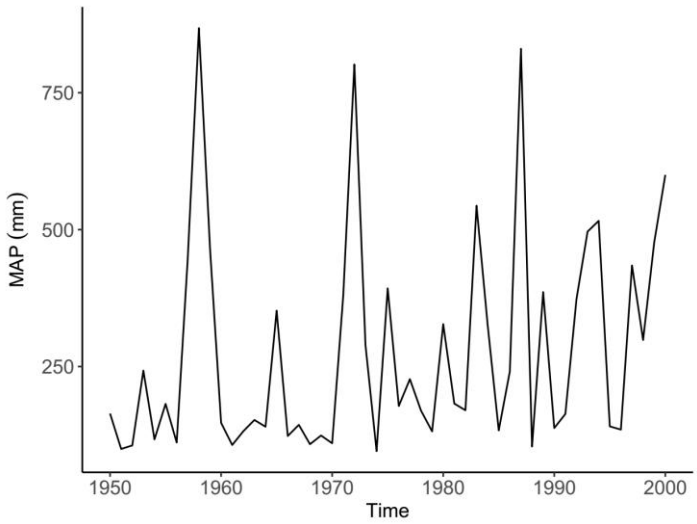
Ignacio Távara







Locuto


MAP (mm)
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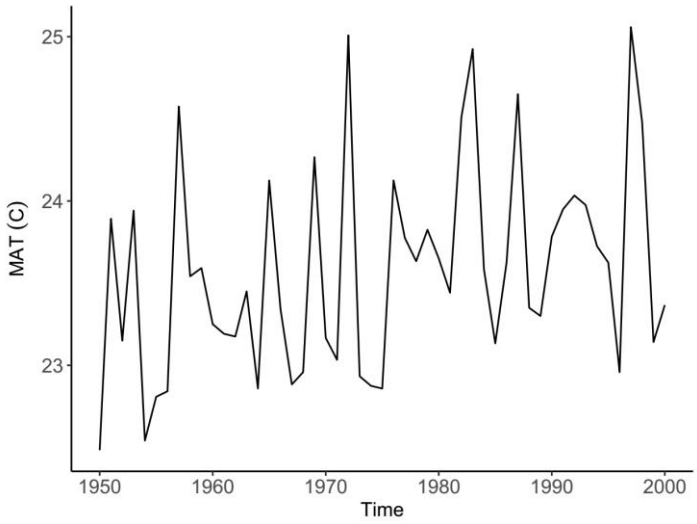
MAT (C)
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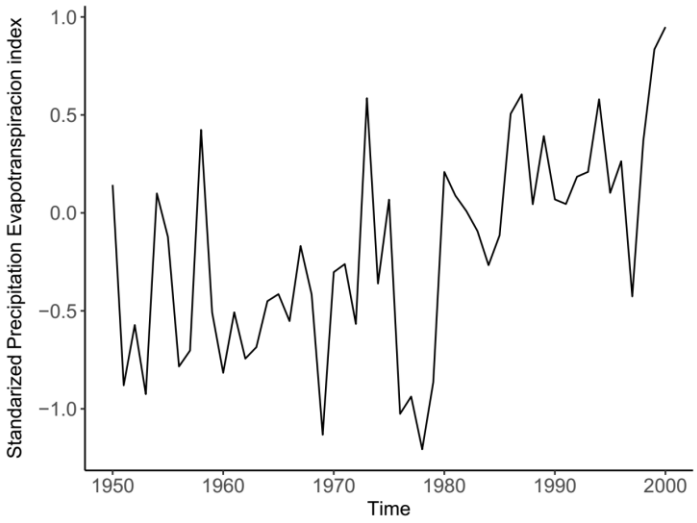
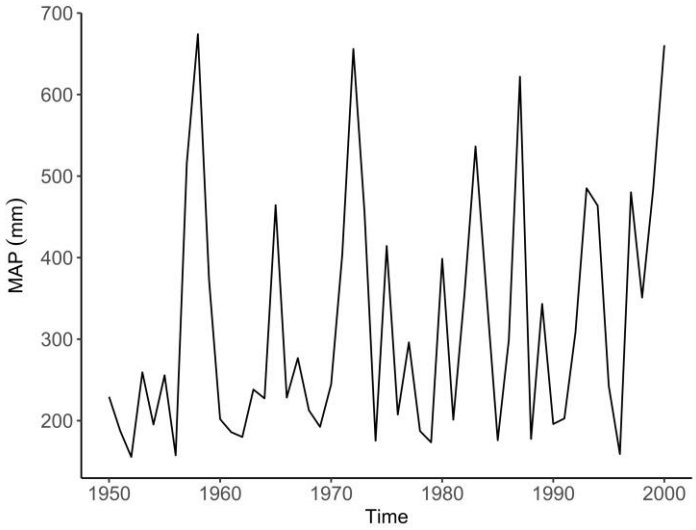
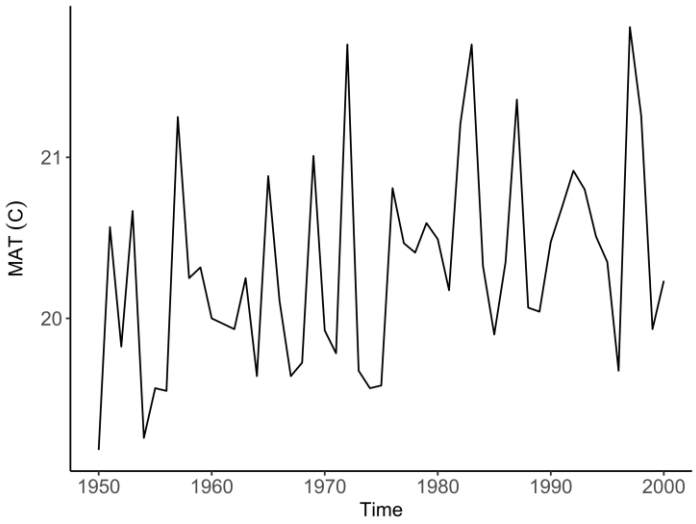
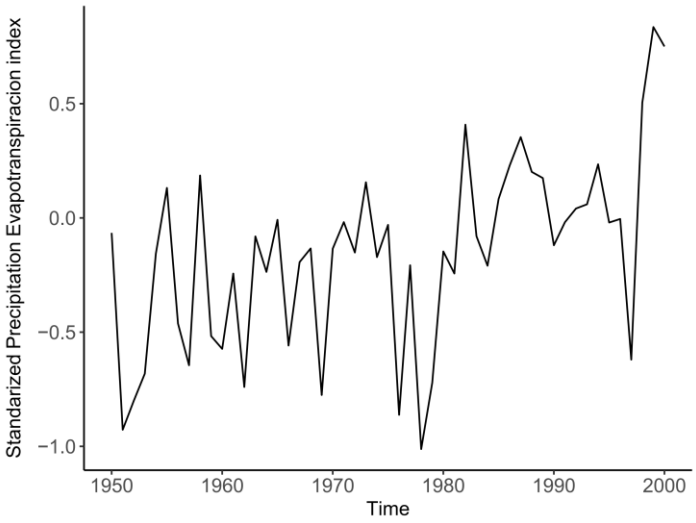
Time


Standarized Precipitation Evapotranspiracion index
1.0
0.5
0.0
−0.5
−1.0
1950
1960
1970
1980
1990
2000
Time

Rio Seco


MAP (mm)
700
600
500
400
300
200
1950
1960
1970
1980
1990
2000
Time


MAT (C)
21
20
1950
1960
1970
1980
1990
2000
Time


Standarized Precipitation Evapotranspiracion index
0.5
0.0
−0.5
−1.0
1950
1960
1970
1980
1990
2000
Time

Anexo 3

Colección Fotográfica

Figura 3.1: Arboles de algarrobo en la zona de Ñapique Humedo durante la fase seca. Notese la ausencia de nubes debido a la corriente de Humboldt y la circulación de Walker.

Figura 3.2: Arboles de algarrobo en la zona de Ñapique Humedo durante la fase húmeda. Notese la presencia de nubes y agua.

Figura 3.3: Imagen frontal de un algarrobo en la zona de Ñapique Humedo durante la fase seca.

Figura 3.4: Arboles de algarrobo en la zona de Ñapique Humedo durante la fase humeda. Notese la presencia de telarañas en el estrato inferior de la copa.

Figura 3.5: Imagen frontal de un algarrobo en la zona de Quebrada Soledad

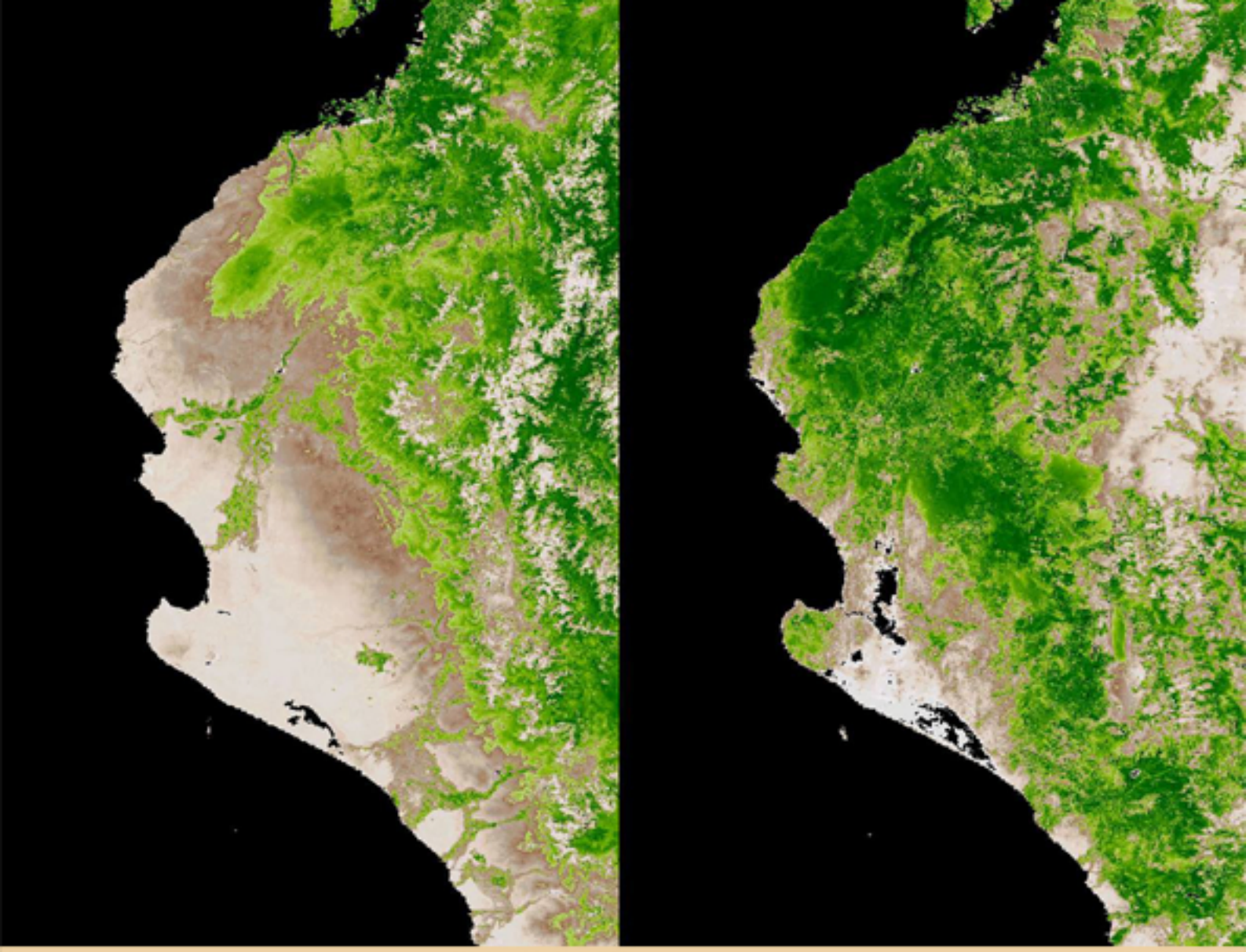
Figura 3.6: Bosque de algarrobo en la zona de Piura durante la fase humeda. Nótese la presencia de herbáceas.

Figura 3.7: Plántula de algarrobo procedente de la zona de Locuto creciendo en invernadero

Figura 3.8: Plántulas de algarrobo de 2 meses de edad en condiciones de alta disponibilidad hídrica tras el experimento de invernadero (aproximadamente 1 metro de altura).

Figura 3.9: Plántulas de algarrobo de 2 meses de edad en condiciones de baja disponibilidad hídrica tras el experimento de invernadero (aproximadamente 0.4 metro de altura).

Figura 3.10: Hojas provenientes algarrobos de 2 meses de edad en condiciones de baja (arriba) y alta (abajo) disponibilidad hídrica tras el experimento de invernadero.



VARIABILIDAD-FENOTÍPICA

CLIMÁTICA

ENSO

ŞEQUÍA

FASE-HÚMEDA

FASE-SECA

CONDUCTIVIDAD

TEMPERATURA

SUELO

BOSQUES

PLASTICIDAD

ÁRBOL

ISLA

AGUA

ZONAS-ARIDAS

FOLIAR

INTRAESPECÍFICA

UNIVERSIDAD DE PIURA

UNIVERSIDAD DE CÓRDOBA